Pennsylvanian brachiopod, fish and conodont faunas from the Caliza Masiva (San Emiliano Formation) at the Mina Profunda area, Cantabrian Zone, NW Spain

Gustavo G. Voldman [a,*], M. Luisa Martínez Chacón [b], Christopher J. Duffin [c], Luis Pedro Fernández [b], Juan L. Alonso [b]

[a] CICTERRA (CONICET–Universidad Nacional de Córdoba), X5016GCB Córdoba, Argentina

[b] Departamento de Geología, Universidad de Oviedo, 33005 Oviedo, Spain

[c] Palaeontology Section, Earth Science Department, The Natural History Museum, Cromwell Road, London SW7 5BD, UK and 146, Church Hill Road, Sutton, Surrey SM3 8NF, England, UK

* Corresponding author. E-mail address: gvoldman@unc.edu.ar (G. Voldman).

Abstract

A rock sample obtained from the Caliza Masiva of the San Emiliano Formation (Bashkirian–early Moscovian) in the Mina Profunda area (NE Villamanín) of the Bodón Nappe (Cantabrian Zone, NW Spain) has yielded numerous brachiopods and fish remains not frequently represented in the fossil record. The brachiopod assemblage comprises 13 taxa and is characterized by phosphatic (*Langella, Orbiculoidea*) as well as exceptionally preserved silicified calcitic elements (a small chonetid, *Composita*, *Crurithyris*, *Lambdarina*, and two minute terebratulids) as the main faunal components. Of special importance is the record of the microbrachiopod *Lambdarina winklerprinsi* nov. sp., which reduces the large Viséan–upper Permian gap in the stratigraphic record of this genus. Conodont elements recovered from the same insoluble residue are indicative of the upper Bashkirian *Idiognathoides sulcatus parvus* Zone. The accompanying fish remains consist of chondrichthyan teeth and scales, an acanthodian scale and osteichthyan tooth-bearing bones, isolated teeth and isolated scales, representing the first Pennsylvanian ichthyoliths analysed from the Cantabrian Zone. The limestone beds with selective silicification in the San Emiliano Formation provide an exceptional opportunity to improve our knowledge on the patterns of life diversity over geological time.

Keywords:

brachiopod

ichthyolith

conodont

San Emiliano Formation

Pennsylvanian

NW Spain

45

1. Introduction

The San Emiliano Formation (Brouwer and van Ginkel, 1964) is a stratigraphic unit of the Bodón and Aramo nappes (in the sense of Alonso et al., 2009), which belong to the Cantabrian Zone, the most external zone of the Iberian Massif in NW Spain (Fig. 1). The San Emiliano Formation is widely recognized due to its rich Bashkirian–early Moscovian fossiliferous content (van Ginkel, 1965; Sánchez de Posada et al. 1996; van Ginkel and Villa, 1996) (Fig. 1). It consists of ca. 1800 m of alternating siliciclastic and carbonate rocks that according to their relative proportions in the type area were grouped into three members, namely the Pinos, La Majúa and Candemuela, from bottom to top (Bowman, 1982). This subdivision is applied elsewhere, with the exception of the study area, where the Pinos Member, the Caliza Masiva (Moore et al. 1971) and the Villamanín beds (Truyols Santonja and Sánchez de Posada, 1983) have been distinguished in the formation (Fernández, 1993). Brachiopods are the most abundant macrofossil in this formation, especially in the La Majúa Member, from which 45 different species of brachiopods have been described (Martínez Chacón and Winkler Prins, 1985).

In the course of a recent stratigraphic and structural study in the Mina Profunda area (Cármenes, NE Villamanín), the Caliza Masiva was sampled for conodonts, for biostratigraphic and palaeothermometric purposes. After acid etching, the various samples were mostly devoid of fossils with the exception of one from the upper part of the unit. This sample yielded a unique microbrachiopod fauna, exceptionally preserved due to the silicification of its shells, a process that is not frequently reported in Carboniferous deposits (Schubert et al. 1997), especially those of the Pennsylvanian. For this reason, the study of the Pennsylvanian microbrachiopods dealt with in this paper sheds some light on the knowledge of a group of rather peculiar Pennsylvanian fossils.

Among these microbrachiopods, the presence of *Lambdarina winklerprinsi* nov. sp. must be emphasized. The stratigraphic distribution of *Lambdarina* is somewhat strange, probably reflecting biases in the fossil record related to the difficulties of finding and extracting these minute calcareous fossils with their shells preserved. Specimens of the genus have mostly been discovered accidentally, collected as silicified remnants from insoluble residues obtained during micropalaeontological procedures. Exceptionally, Muszer (2014) described *L. jugowiensis* (upper Viséan, Sudetes) from numerous non-silicified specimens at different stages of growth, recovered by thermal fragmentation of limestones aided with sodium sulphate (Glauber's salt). Seven of the eight species of *Lambdarina* known to date are restricted to the Tournaisian–Viséan interval, and the eighth species comes from rocks as young as late Permian. Our species, *L. winklerprinsi* nov. sp., late Bashkirian in age, contributes to the filling of the late Viséan–late Permian gap in the fossil record of the genus.

The brachiopod assemblage from Mina Profunda comprises 13 different taxa, including phosphatic (*Langella, Orbiculoidea*) and calcitic shells (a small chonetid, *Lambdarina winklerprinsi* nov. sp., *Composita*, *Crurithyris* and two minute terebratulids) as the most conspicuous elements. Conversely, conodont elements are scarce in the sample, being represented by the cosmopolitan subspecies *Idiognathoides sulcatus parvus* Higgins et Bouckaert, which confirms a late Bashkirian age for the sampled interval. In addition, reports of fish remains as part of the associated fauna are frequent in microfossil collections from the Cantabrian Mountains, yet they have never been analysed in detail before. In the present contribution, the ichthyoliths from Mina Profunda are analysed as well, providing further constraints on the biodiversity and palaeogeographic distribution of the early Pennsylvanian marine faunas from the Cantabrian Mountains.

2. Geological setting

The study area, to the NE of Villamanín (Fig. 2A), belongs to the southern branch of the Bodón Nappe. There, the San Emiliano Formation contains a prominent calcareous unit, the Caliza Masiva of Moore et al. (1971), which forms a several-km-long and up to some 330-m-thick carbonate body, sandwiched between the underlying shales with turbidites and carbonate breccias of the Pinos Member (previously referred to as the Villanueva beds by Bowman, 1982), and the overlying shales with limestones, sandstones and rare coals of the Villamanín beds.

In the recent study of the Mina Profunda area, the Caliza Masiva was found to exhibit a wide range of facies, from carbonate breccias, calclithites and calciturbidites, to massive microbial micrites containing *Donezella* and skeletal limestones (cf. also Riding, 1979). These deposits are suggestive of sedimentation in moderately deep-basin to slope, platform-margin to slope, and shallow-shelf settings, respectively. They are arranged into tens-of-metre-thick cycles bound by minor unconformities.

The Caliza Masiva has been ultimately dated as upper Bashkirian based on its fusulinid content (van Ginkel and Villa, 1996; van Ginkel, 2014), whereas spores point to a Langsettian (Westphalian A) age (Villa et al. 1988).

Contrary to other faunal elements, conodonts are uncommon in the San Emiliano Formation. The scarce findings, reported by Méndez Fernández (1990), consist of a few elements of *Idiognathoides parvus*, *I. macer* (Wirth), and *I. corrugatus* (Harris et Hollingsworth) from successive limestone beds at Fresnedo (Bodón Nappe, to the north of the type area of the formation), and *Idiognathoides* sp., *I. attenuatus* Harris et Hollingsworth and *Spreptognathodus* sp. from the type area of the formation.

3. Material and methods

Several beds of the Caliza Masiva in the Mina Profunda area were sampled for microfossils. Samples, sized 2-3 kg each, were digested in buffered acetic acid following the standard conodont laboratory procedures (Stone, 1987). Only one sample from the upper part of the Caliza Masiva, ca. 40 m below the top of the unit, was productive (Fig. 2B), which led to further intensive resampling. The sampled interval consists of cm- to dm-thick tabular beds of skeletal and lithoclastic pack- to grainstones, amalgamated or interleaved with dark-grey shales to marlstones. Beds display graded and/or parallel laminated divisions and their tops are sharp to gradational with the overlying shales/marlstones. Bioturbation is also scarce. Although field relationships are not clear, the studied beds sharply overlie an interval of massive (microbial?) limestones and pass laterally into similar massive limestones.

Under the microscope, grains comprise mainly crinoid, bryozoan and brachiopod fragments. Sponge spicules are abundant in laminae whereas foraminifers and calcispheres are rare (Fig. 3). Micritic intraclasts and lithoclasts, and peloids are also common. Scattered quartz grains and ooids may be found. Grains are moderately to well sorted, and display a variable, often marked, parallel-to-bedding alignment and/or grading. Laterally, other beds with fish fragments are made of calclithites with microbial micrite lithoclasts and intraclasts, sand to gravel in size, accompanied by large skeletal fragments of the same types described above, plus bivalves and gastropods.

After digesting ca. 18 kg of limestone from these beds, brachiopods, conodonts, and ichthyoliths were recovered. The brachiopod assemblage from the Mina Profunda area is diverse, represented by 13 taxa. It is composed of phosphatic brachiopods (*Langella, Orbiculoidea*) as well as silicified calcitic brachiopods. The phosphatic brachiopods and most of the calcitic brachiopods have very small sizes even in adult stages (Caenanopliinae indet., *Lambdarina, Composita, Crurithyris*, Terebratulidina indet.). The brachiopod assemblage also includes some fragmented medium-sized specimens (*Maemia, Alexenia,*

144 *Anthracospirifer, Anthracothyrina, Spiriferellina*). The conodont elements, despite being
145 scarce, provide further biostratigraphic constraints. Images of the microfossils were obtained
146 with a Zeiss Axiocam 506 camera attached to an Axio Scope.A1 petrographic microscope
147 (Departamento de Geología, Universidad de Oviedo). Image stacking was conducted with
148 Zerene Stacker and Adobe Photoshop.
149 The ichthyoliths represent a low diversity chondrichthyan and osteichthyan fauna
150 mostly comprising isolated teeth and scales. Most of the specimens are highly fractured. The
151 less damaged were studied under the light microscope, and imaged at the NHMUK using a
152 Jeol JSM-IT500 Scanning Electron Microscope with an acceleration voltage of 15kv at a
153 pressure of 40 Pa.
154 All specimens are housed in the Departamento de Geología, Universidad de Oviedo
155 (prefix DGO). They are preserved on microscope slides and some ichthyoliths on SEM stubs.
156

157 **4. Brachiopod silicification**

158 The silicification of the brachiopods from Mina Profunda is usually incomplete,
159 diminishing its preservation potential. In particular, all of the shells of *Lambadarina*
160 *winklerprinsi* nov. sp. from our collection lack their posterior extremity. Moreover, the
161 fidelity of the replacement is rather variable, with some specimens presenting gross beekite
162 rings and siliceous grains agglutinated onto the specimen. The shell microstructure is usually
163 not preserved, although the perforations of punctae of the terebratulids and *Spiriferellina,* and
164 the fine hollow spines of the latter genus are preserved.
165 According to Butt and Briggs (2011), beekite rings are formed in conditions of limited
166 or sporadic silica supply. This circumstance is also probably reflected by the incomplete
167 silicification of our specimens. As to the silica source, although no detailed study has been
168 carried out, neither a biogenic origin from sponge spicules nor an input from the hydrothermal

fluids responsible for the dolomitization and ore mineralization in the Mina Profunda area can be discarded.

5. Systematic palaeontology

5.1. Brachiopods

Phylum Brachiopoda Duméril, 1805

Subphylum Linguliformea Williams, Carlson, Brunton, Holmer et Popov, 1996

Class Lingulata Gorjansky et Popov, 1985

Order Lingulida Waagen, 1885

Superfamily Linguloidea Menke, 1828

Family Lingulidae Menke, 1828

Genus ***Langella*** Mendes, 1961

Type species: *Lingula imbituvensis* de Oliveira, 1930.

Langella? sp.

Figs. 4(A–C)

Material: One ventral valve (DGO 25486), two dorsal valves (DGO 25487-25488) and a valve fragment (DGO 25489).

Description: Shell elongated, drop-shaped, and biconvex. Ventral valve with narrow pedicle groove. Dorsal valve with a small, undivided pseudointerarea which results in a rounded, thickened posterior margin. Ornamentation of dense growth lines. Both valves are thin and the internal characters are not impressed.

Measurements in mm: DGO 25486: L=1.75, W=1.03; DGO 25487: Ld=1.78, W=1.35; DGO 25488: Ld=2.03, W=1.21.

Remarks: The general external shape of the present material evokes the genera *Langella* or *Barroisella* Hall et Clarke. The preservation of the Cantabrian specimens, with a thin shell

194 which does not show any internal characteristics, prevents us from making a more precise
195 identification. The specimens are assigned, with some doubts, to *Langella* because the shell of
196 this genus seems to be thinner and with internal structures less marked than those of the genus
197 *Barroisella*.
198 **Occurrence:** The genus was first described for the Permian of Paraná, Brazil (de Oliveira,
199 1930). Sun and Baliński (2008) described it from the middle Tournaisian of southern China.
200 The Cantabrian specimens could fill the large temporal gap between both records.
201
202 Superfamily Discinoidea Gray, 1840
203 Family Discinidae Gray, 1840
204 Genus ***Orbiculoidea*** d'Orbigny, 1847
205 **Type species:** *Orbicula forbesii* Davidson, 1848.
206 *Orbiculoidea* sp.
207 Figs. 4(D–F)
208 **Material:** Two incomplete ventral valves, a juvenile ventral valve and ca. 12 valve fragments,
209 mostly ventral, and a few juveniles, DGO 25490-25493.
210 **Description:** Ventral valve with holoperipheral growth, subcircular in outline, low cone
211 shaped, with subcentral apex; pedicle slit closed anteriorly by listrium; foramen at posterior
212 end of listrium, continued as internal tube to open in front of posterior margin (Fig. 4E_2).
213 Larval shell smooth, subcircular, reaching about 0.5 mm in length; postlarval shell
214 ornamented with well-developed, high concentric ridges (7 in 0.5 mm). The best preserved
215 specimen is 1.75 mm in length.
216 **Remarks:** *Orbiculoidea* is a well-known genus generally represented in Carboniferous fossil
217 localities, though often by only a few specimens. It is known from the San Emiliano
218 Formation at its type area (*Orbiculoidea* sp.: Carballeira et al. 1985) and from the Villamanín

beds, N of Villamanín (unpublished data). All the above specimens are significantly larger and have an ornamentation finer than those studied in this work. Moreover, the small size and strong concentric ornamentation distinguishes the present material from the other species of the genus.

Occurrence: *Orbiculoidea* is cosmopolitan ranging from Silurian (with doubts from Ordovician) to Permian.

Subphylum Rhynchonelliformea Williams, Carlson, Brunton, Holmer et Popov, 1996

Order Productida Sarytcheva et Sokolskaya, 1959

Suborder Chonetidina Muir-Wood, 1955

Superfamily Chonetoidea Bronn, 1862

Family Anopliidae Muir-Wood, 1962

Subfamily Caenanopliinae Archbold, 1980

Caenanopliinae gen. et sp. indet.

Fig. 4(G)

Material: An internal mould of both valves, DGO 25494.

Description: Shell very small (L=1.14, W=1.32, measurements of the only specimen), strongly concavo-convex, subcircular in outline, ears incomplete. Marks of external costae seem to occur in the anterior region of the ventral internal mould. Ventral interior with short and high median septum. Dorsal interior without median septum; with long and high inner socket ridges supporting small cardinal process; anderidia slightly marked and anteriorly divergent at a large angle; without accessory septa; with relatively large endospines arranged in five pairs of radial rows; the endospines closest to the median axis are the largest.

Remarks: The very small size, almost equidimensional shell and the absence of a dorsal median septum suggest that our specimen is a member of the Family Anopliidae. The

probable costate exterior points towards the subfamily Caenanopliinae, particularly to the genera *Globosochonetes* Brunton and *Subglobosochonetes* Afanasjeva. These two genera are distinguished on the presence or absence of accessory septa; the Tournaisian *Subglobosochonetes* lacks accessory septa and is the most similar to specimen DGO 25494. Our specimen also resembles the Permian genus *Neotornquistia* Afanasjeva of the subfamily Anopliinae, as a smooth exterior surface cannot be discarded. However, DGO 25494 could be a juvenile form that has not yet developed diagnostic generic characters. These uncertainties prevent us from making a more accurate determination.

Occurrence: The subfamily Caenanoplinae ranges in age from the Lochkovian (Devonian) to the Kungurian (Permian). *Globosochonetes* is the most common genus of this subfamily in the Carboniferous of the Cantabrian Zone. It occurs in several localities of the San Emiliano Formation, including the Moscovian Villamanín beds (Villa et al. 1988).

Suborder Productidina Waagen, 1883

Superfamily Productoidea Gray, 1840

Family Productellidae Schuchert, 1929

Subfamily Plicatiferinae Muir-Wood et Cooper, 1960

Tribe Semicostellini Nalivkin, 1979

Genus ***Maemia*** Lazarev, 1997 (in Brunton and Lazarev)

Type species: *Maemia chaykensis* Lazarev 1997 (in Brunton and Lazarev).

Maemia cf. *archboldi* Martínez Chacón et Winkler Prins, 2008

Figs. 4(J), 5(B)

Material: One articulated specimen (DGO 25495) and two isolated ventral valves (DGO 25496-25497).

Description: Shell small, almost equidimensional (L=7.1 mm, W=7.3 mm, Th=2.95 mm in the articulated specimen), with subcircular outline. Ventral valve strongly convex, with umbo inflated, rounded and extending behind the hinge; ornamentation of irregular concentric rugae slightly lamellose; a row of spines is developed along the hinge and others, relatively large, seemingly straight, are arranged in quincunx. Dorsal valve with lamellae in its anterior part, pits corresponding to the spines of the opposite valve and a few spines thinner than those of the ventral valve.

Remarks: The specimens are very similar to *M. archboldi* by their ventral convexity, ornamentation with concentric, lamellose rugae and large spine bases scattered in quincunx; and dorsal valve with a few spines thinner than the ventral ones. Their incomplete preservation prevents us from making a more precise determination. Their very small size and undeveloped trail suggest that they could be juveniles of this species.

Our specimens also resemble *Quasiavonia aculeata* (Sowerby, 1814), a species frequently described or cited from the Carboniferous of the Cantabrian Zone (Winkler Prins, 1968; Martínez Chacón, 1979; Martínez Chacón and Winkler Prins, 1985, 2007), although part of this material has been synonymized with *M. archboldi* (Martínez Chacón and Winkler Prins, 2008). The main differences between the genera *Quasiavonia* and *Maemia* are the geniculation of both valves, the deeper corpus cavity and the dorsal adductor scars raised with median-curving crests of *Maemia*. None of these characteristics can be observed in the present material. However, the small size, inflated ventral valve and coarse spine bases quincunxially arranged, widely separated from each other, suggest co-specificity with *M. archboldi*, although with some doubts.

Occurrence: *M. archboldi* is known from the Pennsylvanian (late Bashkirian–early Moscovian) of the Cantabrian Zone (Martínez Chacón and Winkler Prins, 2008).

293 Family Productidae Gray, 1840

294 Subfamily Productinae Gray, 1840

295 Tribe Spyridiophorini Muir-Wood et Cooper, 1960

296 Genus ***Alexenia*** Ivanova in Ivanov, 1935

297 **Type species:** *Alexenia reticulata* Ivanova in Ivanov, 1935.

298 *Alexenia?* sp.

299 Fig. 5(D)

300 **Material:** A single specimen, very deformed, crushed and incomplete, DGO 25498.

301 **Description:** Medium-sized shell (L>17 mm, W>25,7 mm), ears large, flat and strongly
302 differentiated, frontal commissure uniplicate. Ventral valve with ears sharply separated from
303 the disc by a deep sulcus and a ridge on the flanks, which carries a row of thick spines with
304 their diameter increasing strongly forward. Ornamentation semireticulate, with rounded
305 costae (7 in 5 mm on the disk) becoming coarse on the trail (5 in 5 mm); the spines are few in
306 number: one row on the ridges on the flanks, one row along the hinge and several scattered
307 over the valve.

308 **Remarks:** Given the conditions of preservation of the specimen, it is impossible to know its
309 original dimensions, even approximately. Its external characteristics suggest the genus
310 *Alexenia*, but we do not know its interior. In the Cantabrian Mountains, the species *Alexenia?*
311 *delepinei* Martínez Chacón et Winkler Prins, 2015 has been described from coeval deposits.
312 The latter species differs from the typical *Alexenia* in the arrangement of the dorsal muscle
313 field, placed on the bottom of the valve, bordered medianly by parallel ridges lower than
314 those usually found in *Alexenia.* On the basis of this character, Martínez Chacón and Winkler
315 Prins (2015) consider that *Alexenia? delepinei* could belong to a new genus at the base of the
316 Tribe Spyridiophorini or perhaps the earliest representative of *Alexenia*, but which has not yet
317 developed the elevated muscle platforms typical of other species in the genus. As we do not

know the dorsal interior of the specimen on hand, we attribute the specimen from Mina Profunda to *Alexenia* with reservations. Moreover, despite the fact that it resembles *A.? delepinei*, its larger size and poor preservation precludes a confident comparison. Therefore, we prefer to leave its classification open.

Occurrence: *Alexenia* is a genus known from the late Moscovian to Kasimovian of Eurasia. *Alexenia? delepinei* is known from the late Bashkirian–early Moscovian interval of the Cantabrian Mountains. Amongst other species from the Cantabrian Zone, *A. arbizui* Martínez Chacón, 1979, known from the upper Kashirsky (lower Moscovian) has a dorsal interior typical of *Alexenia*.

Order Rhynchonellida Khun, 1949

Superfamily Lambdarinoidea Brunton et Champion, 1974

Family Lambdarinidae Brunton et Champion, 1974

Subfamily Lambdarininae Brunton et Champion, 1974

Genus ***Lambdarina*** Brunton et Champion, 1974

Type species: *Lambdarina manifoldensis* Brunton et Champion, 1974.

Lambdarina winklerprinsi nov. sp. Martínez Chacón

Figs. 6(A–J)

?1993. *Lambdarina* sp. - Martínez Chacón et Winkler Prins, p. 576, pl. 2, fig. 6.

Derivation of the name: In honour of Dr. Cornelis Winkler Prins (Naturalis Museum, Leiden), colleague and friend, recently passed away (18 April 1939–27 June 2019). He guided MLMCh masterfully in her beginnings in the study of Carboniferous brachiopods. With her grateful memory.

Holotype: shell with its posterior part not preserved, DGO 25506 (Fig. 6B$_{1\text{-}2}$). **Paratypes:** 22 shells also with the posterior part not preserved due to incomplete silicification, one complete

343 internal mould of a juvenile specimen, and 4 incomplete internal moulds, DGO 25499-25505,
344 25507-25514.
345 **Type locality:** 370 m to the SW of Mina Profunda (42º57'43''N, 5º36'14''W), Cármenes
346 (León, NW Spain), San Emiliano Formation, upper part of the Caliza Masiva (after Moore et
347 al. 1971), upper Bashkirian.
348 **Diagnosis:** *Lambdarina* with wide and quite long lobes, rounded at the end; dorsal valve with
349 deep median sulcus; ventral valve with very weak or absent median sulcus, usually without
350 median ridge. Dental plates long, supporting the teeth on their anterior end; inner socket
351 ridges strong and high, joined to the notothyrial platform.
352 **Description:** Small shell (the largest specimen reaches little more than 2.07 mm in length,
353 DGO 25502), approximately equidimensional or slightly transverse in adults, and a little
354 elongated in juveniles, dorsibiconvex, smooth, heart-shaped, bilobate, with lobes starting in
355 the anterior half of the length in larger specimens in which the margins of the lobes are more
356 or less parallel, rounded at the front; angle of lobe bifurcation increases with age, ranging
357 from 65 to 98 degrees (this last value in the specimen DGO 25500, Fig. 6G). Ventral valve
358 with umbo long and narrow, tube-like, slightly curved dorsally; the rounded and relatively
359 large foramen is situated at the apex of the tube-like umbo (DGO 25499, Fig. 6A_2) or slightly
360 displaced in a dorsal direction (DGO 25507, Fig. 6C_2); median sulcus very weak or absent,
361 usually without median ridge. Dorsal valve rather shorter than ventral valve, with well-
362 developed and deep median sulcus.
363 Ventral interior with strong teeth and long dental plates supporting the teeth on their
364 anterior end and not extending anteriorly beyond the teeth. Dorsal interior with deep dental
365 sockets, limited by strong and long inner socket ridges, united to the notothyrial platform; the
366 notothyrial platform is depressed in its ventral side, on its posterior end seems to appreciate
367 the presence of a small cardinal process (Fig. 6A_2).

368 **Measurements:** Are on Table 1. Owing to the fact that all the shells are devoid of their apical
369 region, the measured length is less than the actual value.
370 **Ontogeny:** With ontogeny, the specimens show changes in the shell form and in the size of
371 the lobes. Specimens smaller than 1.07 mm in length are not present in our collection. The
372 smaller specimens have a triangular outline, are slightly elongated, and the lobes only appear
373 in the anterior end; the dorsal medial sulcus starts to develop. The shell acquires a heart-
374 shaped outline during the process of growth, becoming slightly transverse, and the lobes start
375 a little ahead of half the length of the shell, increasing their divergence. In adult specimens,
376 the typical characteristics for the species are developed: deep dorsal medial sulcus, long lobes
377 that reach a little more than ½ of the length of the shell, and a large angle of divergence.
378 **Comparison:** So far, eight species have been included in the genus. *L. jugowiensis* Muszer is
379 most similar to *L. winklerprinsi* nov. sp. by its general shape, development of bilobation and
380 absence of a median ridge in the ventral sulcus. However, it differs from the species described
381 here in having a slightly elongated shell and shorter and less separate lobes. Both *L.*
382 *manifoldensis*, and *L. glaphyra* Basset et Bryant also have outlines and bilobations similar to
383 those of *L. winklerprinsi.* However, these two species differ from our species in having the
384 ventral sulcus well developed and with a median ridge. *L. sinensis* Baliński et Sun, *L. babini*
385 Martínez Chacón, and *L. granti* Nazer differ from our species by possessing a less lobate
386 shell; the last two species also have a well-developed ventral sulcus with a median ridge. On
387 the other hand, *L. brownendensis* Morris and *L. iota* Grant are clearly distinguishable by their
388 long, narrow and widely separated lobes.
389 **Remarks:** *Lambdarina* is a genus essentially known from the Viséan, based on the records of
390 *L. manifoldensis* and *L. brownendensis* (early Viséan, North Staffordshire, England), *L. granti*
391 (upper Viséan, Queensland), *L. jugowensis* (late Viséan, Sudetes, SW Poland), and *L. babini*
392 (late Viséan, Los Santos de Maimona, Badajoz, SW Spain). Two species are described from

393 the Tournaisian, *L. sinensis* (middle Tournaisian, Guizhou Province, South China), the oldest
394 known to date, and *L. glaphyra* (late Tournaisian, Belgium). A temporal gap of 56 Ma
395 separates the former species with *L. iota* (Late Permian, Hydra Island, Greece). *L.*
396 *winklerprinsi* nov. sp., from the late Bashkirian, partially fills this large gap, being the first
397 species of *Lambdarina* known from the Pennsylvanian.
398 This is not the first time that the genus *Lambdarina* is mentioned in the late Bashkirian
399 of the Cantabrian Zone. Martínez Chacón and Winkler Prins (1993) cited a single incomplete
400 specimen from the Valdeteja Formation (Valdeteja, Bodón Nappe, several km to the east of
401 the studied area), as *Lambdarina* sp. The specimen has not been described and the only figure
402 published is insufficient for definitive comments. However, it seems similar to *L.*
403 *winklerprinsi* in outline, both have the same age and come from nearby locations, although of
404 different formations. For these reasons, we consider, although with doubts, that the specimen
405 from Valdeteja Formation assigned to *Lambdarina* sp. could belong to *L. winklerprinsi*.
406 The material of *L. winklerprinsi* includes internal moulds of the two joined valves,
407 some of which reveal important details of the interior. This is the first record of internal
408 moulds of representatives of the genus *Lambdarina*.
409 **Occurrence:** As indicated above, the stratigraphic range of *Lambdarina* is middle
410 Tournaisian–upper Permian. *L. winklerprinsi* nov. sp. was recovered from the upper
411 Bashkirian rocks.
412
413 Order Athyridida Boucot, Johnson et Staton, 1964
414 Suborder Athyrididina Boucot, Johnson et Staton, 1964
415 Superfamily Athyridoidea Davidson, 1881
416 Family Athyrididae Davidson, 1881
417 Subfamily Spirigerellinae Grunt, 1965

418 Genus ***Composita*** Brown, 1845

419 **Type species:** *Spirifer ambiguus* Sowerby, 1822.

420 *Composita* sp.

421 Fig. 4(N)

422 **Material:** 3 internal moulds of both valves and 4 incomplete silicified shells, DGO 25515-

423 25516, DGO 25526-25527.

424 **Description:** Shell ventribiconvex, subovate or tear-drop shaped, slightly elongated, widest

425 near mid-length, without fold and sulcus, anterior commissure rectimarginate. Shell smooth,

426 with concentric lines of growth marked in the anterior part of the internal mould of both

427 valves.

428 Ventral interior with dental plates thin and short, very close to the side wall. Between

429 them and extending further forward is the muscle field, depressed at the bottom of the valve,

430 little marked and divided by a low and wide myofragma.

431 Dorsal interior with cardinal plate short and wide, ventrally concave, projecting

432 backwards and with two small diductor pits; from its anterior part rose the crura. The adductor

433 muscle field is narrow and long; at its posterior end, it is divided by a very short, narrow and

434 low myofragma, followed by a median depression; the two pairs of muscles are practically

435 parallel, the middle pair is elevated above the bottom of the valve and the outermost pair is

436 depressed.

437 **Remarks:** By its smooth shell and the internal characteristics observed, the present material

438 seems to belong to the genus *Composita*, but the poor preservation of the specimens prevents

439 attribution to species level.

440 **Occurrence:** *Composita* is a cosmopolitan genus ranging from the Upper Devonian to the

441 upper Permian. In the Cantabrian Zone it has been reported and described from the San

442 Emiliano Formation (Carballeira et al. 1985) and the Calizas del Cuera (Martínez Chacón,
443 1990) of upper Bashkirian–upper Moscovian age.
444
445 Order Spiriferida Waagen, 1883
446 Suborder Spiriferidina Waagen, 1883
447 Superfamily Ambocoelioidea George, 1931
448 Family Ambocoeliidae George, 1931
449 Subfamily Ambocoeliinae George, 1931
450 Genus ***Crurithyris*** George, 1931
451 **Type species:** *Spirifer urei* Fleming, 1828.
452 *Crurithyris* cf. *urei* (Fleming, 1828)
453 Figs. 4(H–I, K–M)
454 **Material:** 20 shells incompletely silicified, 10 internal moulds of two valves and 1
455 incomplete dorsal valve showing part of the interior, DGO 25517-25525.
456 **Description:** Small ventribiconvex shell with hinge line less than width of shell, high
457 apsacline ventral interarea and short catacline dorsal interarea; subcircular outline with width
458 slightly longer than length; both valves with very weak sulci. The larger specimen measures
459 1.46 mm in length and 1.67 mm in width; the smallest measures 0.53 mm in length and 0.61
460 mm in width. Ventral interior with dental ridges and without dental plates; muscle scars well
461 impressed, confined to the posterior region and with indistinct adductors and diductors.
462 Dorsal interior with a small, triangular cardinal process raised on a short notothyrial platform
463 in the apex of the inner socket ridges; inner socket ridges strong, elevated; crural bases united
464 to valve floor by short crural plates; crura subparallel, extending forward, they are long but
465 their end cannot be observed because the dorsal valve is broken (Fig. 4.L).

Remarks: The specimens on hand closely resemble the type species *C. urei* from which they differ slightly because of the less convex ventral valve, the narrower hinge and the less developed median groove of both valves. Our specimens also look like *C. planoconvexa* (Shumard, 1855), from which they are distinguished by their less flattened dorsal valve.

Occurrence: *C. urei* is typically known from the Viséan of Great Britain and the Tournaisian-upper Viséan of the Moscow Basin (Brunton, 1984). It has been cited or described from the Tournaisian to the upper Bashkirian of the Cantabrian Zone (Martínez Chacón and Winkler Prins, 1985; Martínez Chacón and Sánchez de Posada, 2018).

Superfamily Spiriferoidea King, 1846

Family Spiriferidae King, 1846

Subfamily Sergospiriferinae Carter, 1974

Genus ***Anthracospirifer*** Lane, 1963

Type species: *A. birdspringensis* Lane, 1963.

Anthracospirifer sp.

Fig. 5(F)

Material: A single fragment of ventral valve, DGO 25528.

Description: The specimen presents the ventral interarea denticulated. The ornamentation consists of strong, thick and subangular costae, the grooves that separate them are similar to the costae; the costa that limits the sulcus is thicker than the rest and bifurcates once into the sulcus and twice to the flank; the next costa on the flank bifurcates once towards the middle and towards the side; the next two bifurcate once to the side.

Remarks: The ornamentation of the fragment on hand fits into those of the genus *Anthracospirifer*. However, the poor preservation of the specimen prevents us from making a more precise attribution.

Occurrence: *Anthracospirifer* is a cosmopolitan genus known throughout the Carboniferous. In the Cantabrian Zone it is known from the upper Bashkirian of the San Emiliano Formation (Martínez Chacón and Winkler Prins, 1985), and from upper Bashkirian–lower Moscovian strata of the Calizas del Cuera (Martínez Chacón and Bahamonde, 2008).

Family Choristitidae Waterhouse, 1968

Subfamily Angiospiriferinae Legrand-Blain, 1985

Genus ***Anthracothyrina*** Legrand-Blain, 1984

Type species: *Brachythyrina (Anthracothyrina) perextensa* Legrand-Blain, 1984.

Anthracothyrina? sp.

Fig. 5(E)

Material: One incomplete ventral internal mould, DGO 25529.

Description: Ventral valve convex, with sulcus wide and relatively deep in its front; interarea denticulate; ornamentation of rounded costae which widened to the front, the 3 costae closest to the sulcus bifurcate, the rest are simple; 4-5 costae are counted in 5 mm at the front of the shell. Vascular impressions ramiform at their beginning. L>21.14 mm, W~32 mm.

Remarks: The genus has been described from many localities exposing the the San Emiliano Formation, including the region N of Villamanín, and especially by the species previously described as *Brachythyrina pinica* Martínez Chacón, 1978. The characteristics that can be seen in our specimen point towards the genus *Anthracothyrina*. The distinctive vascular impressions of this genus are reticulate, but only their beginnings are visible in our specimen. For this reason, the attribution to the genus is done with some reservations. The species from Mina Profunda differs from *A. pinica* in its larger number of thinner, bifurcating ribs.

Occurrence: The genus *Anthracothyrina* is known in the Cantabrian Zone from the upper Bashkirian to the Bashkirian/Moscovian boundary, as is the genus *Anthracospirifer*.

Order Spiriferinida Ivanova, 1972

Suborder Spiriferinidina Ivanova, 1972

Superfamily Pennospiriferinoidea Dagys, 1972

Family Spiriferellinidae Ivanova, 1972

Genus ***Spiriferellina*** Frederiks, 1924

Type species: *Terebratulites cristatus* von Schlotheim, 1816.

Spiriferellina sp.

Fig. 5(C)

Material: A fragment of a ventral valve, DGO 25530.

Description: The specimen is a very incomplete ventral fragment. Only the sulcus is preserved with the plicae that limit it and one more plica on the left side. Length of the preserved part measures 8.05 mm. Sulcus deep, subangular, smooth and with abrupt walls; sulcus-bounding plicae, coarser than the lateral plicae, all of them, strong, coarse and subangular; micro-ornamentation of imbricate and close growth laminae, 8-9 in 3 mm, wearing very fine, hollow spines. Shell punctate with coarse punctae. Interior unknown.

Material: The observed characteristics of the specimen coincide with those of *Spiriferellina* but the fragmentary preservation of the material precludes a specific identification.

Occurrence: *Spiriferellina* is a cosmopolitan genus ranging from the Mississippian to the upper Permian. In the Cantabrian Zone, the species *S. multispinosa* Martínez Chacón, 1991, is known from the Podolskian (upper Moscovian) beds of the Calizas del Cuera.

Order Terebratulida Waagen, 1883

Suborder Terebratulidina Waagen, 1883

Terebratulidina gen. et sp. indet. 1

Fig. 4(O)

Material: Three articulated specimens more or less complete and 1 internal mould of both valves, DGO 25531-25533.

Description: Shell small (DGO 25531: L>1.64, W=1.78), endopunctate, biconvex, triangular in outline, slightly transverse, with the maximum width located almost in front of the shell, anterior commissure slightly unisulcate. Dorsal valve with a median sulcus that originates towards half the length of the valve and which widens and deepens in the front, trending ventrally. Ventral valve practically smooth, presenting only a very slight median elevation corresponding to the sulcus of the other valve.

Both valves without median septum. Ventral valve with pedicle collar and very short dental plates. Dorsal valve with strong crural plates.

Remarks: The endopunctate nature and the form of the shell suggest that these specimens belong to the Order Terebratulida and the Suborder Terebratulidina, the only suborder with Palaeozoic representatives. The lack of knowledge of its loop and other details of the dorsal interior prevent us from a more precise diagnosis.

Terebratulidina gen. et sp. indet. 2

Fig. 5(A)

Material: One fragment of the anterior part of a ventral valve, DGO 25534.

Description: Shell endopunctate. The fragment shows a narrow median sulcus with rounded bottom and parallel sides which divides the valve in two wide lateral lobes.

Remarks: The preserved fragment resembles the species *Girtyella llopisi* Martínez Chacón et Winkler Prins, 2008, described from the late Bashkirian of the Valdeteja Formation at Latores (SW of Oviedo). The poor preservation of the single fragment does not allow a more confident identification.

566

567 *5.2. Conodonts*

568 Class Conodonta Pander, 1856

569 Order Ozarkodinida Dzik, 1976

570 Family Idiognathodontidae Harris et Hollingsworth, 1933

571 Genus ***Idiognathoides*** Harris et Hollingsworth, 1933

572 **Type species:** *Idiognathoides sinuatus* Harris et Hollingsworth, 1933.

573 *Idiognathoides sulcatus parvus* Higgins et Bouckaert, 1968

574 Fig. 7

575 1968. *Idiognathoides sulcata parva* subnov. sp. - Higgins et Bouckaert, p. 41, pl. 6, figs. 1–6.

576 1975. *Idiognathoides sulcatus parvus* Higgins et Bouckaert - Higgins, p. 56, pl. 13, figs. 13–

577 14, 18, pl. 14, figs. 2–3.

578 1990. *Idiognathoides parvus* (Higgins et Bouckaert) - Méndez Fernández, p. 100–101, pl. 9,

579 figs. 15–16.

580 1999. *Idiognathoides sulcatus parvus* Higgins et Bouckaert - Nemyrovska, p. 72, pl. 3, figs. 6,

581 16.

582 2003. *Idiognathoides sulcata parva* Higgins et Bouckaert - Wang and Qi, pl. 1, figs. 13, 18.

583 2016. *Idiognathoides sulcatus parvus* Higgins et Bouckaert - Qi et al., fig. 11J.

584 2017. *Idiognathoides sulcatus parvus* Higgins et Bouckaert - Nemyrovska, pl. 2, fig. 2.

585 **Material:** One complete P_1 element and two P_1 fragments (DGO25535-25537).

586 **Description:** The free blade is straight and of approximately the same length as the platform,

587 and carries 8-10 discrete denticles that slightly decrease in height towards the platform

588 junction. The platform is divided by a narrow groove that separates two noded parapets, the

589 rostral (outer) one is a prolongation of the blade and continues up to the dorsal tip of the

590 element, the caudal (inner) parapet is less developed, being slightly lower in height and

591 tapering posteriorly to the rostral parapet at ca. 3/4 the length of the platform. The basal cavity
592 is deep and occupies the entire length of the element, being narrow in the free blade and
593 expanded under the platform. The basal cavity tip is not apparently centred, but situated
594 below the oral groove. The lower portion of the lateral walls of the element, particularly at the
595 free blade, are slightly flexed inwards.
596 **Remarks:** *Idiognathoides sulcatus parvus* differs from *Idiognathoides sulcatus sulcatus*
597 Higgins et Bouckaert by possessing a shorter inner parapet, though as it is difficult to
598 distinguish them in some cases, transitional forms have been adopted. *Idiognathoides*
599 *postsulcatus* Nemyrovska is also distinguished by its equal length parapets, very convex
600 platform sides, and shallow groove. *Idiognathoides macer* (Wirth) presents ridges in the
601 ventral section of the inner parapet, not nodes as in *I. s. parvus*.
602 **Occurrence:** The genus *Idiognathoides* characterizes most of the Bashkirian and lower
603 Moscovian rocks of Europe and Asia. *Idiognathoides sulcatus parvus* is an index fossil in
604 South Guizou of China, where its first record marks the beginning of the homonymous
605 biozone, and ranges into the overlying *Streptognathodus expansus* Zone (Wang and Qi, 2003;
606 Qi et al. 2016). In the Donets Basin of Ukraine, the FAD of *I. sulcatus parvus* occurs in the
607 *Idiognathodus sinuosus* Zone (Prikamian, upper middle Bashkirian), ranging up to the
608 *Idiognathoides tuberculatus–I. fossatus* Zone (Cheremshankian, middle upper Bashkirian)
609 (Nemyrovska, 2017; Nemyrovska and Hu, 2018). In the Cantabrian Zone, it was previously
610 described from the San Emiliano Formation at Fresnedo (a stratigraphic section situated in the
611 Sobia nappe) and from the lower Picos de Europa Formation at Les Llaceries (Picos de
612 Europa Unit), and referred by Méndez Fernández (1990) to the upper Bashkirian and lower
613 Moscovian, respectively. The records of both '*Str.' expansus* and '*Str.' suberectus* in the
614 Valdeteja Formation (Nemyrovska, 2017), which interdigitates with the San Emiliano
615 Formation, conceivably reinforce an early late Bashkirian age for our faunal assemblage.

616

617 *5.3. Fishes*

618 Class Chondrichthyes Huxley, 1880

619 Order Ctenacanthiformes Glikman, 1964

620 Family indet.

621 Genus ***Glencartius*** Ginter et Skompski, 2019

622 **Type species:** *Ctenacanthus costellatus* Traquair, 1884.

623 *Glencartius costellatus* (Traquair, 1884)

624 Fig. 8(A–B)

625 **Material:** Two incomplete, isolated teeth, DGO 25459 and DGO 25462.

626 **Description:** The largest specimen (DGO 25459; Fig. 8A) measures 2.0 mm mesiodistally
627 along the labial border and 0.9 mm labiolingually; it has a cladodont organisation. The tooth
628 is quite elongate mesiodistally. The cusps have sustained much damage and only their bases
629 are present. A relatively large central cusp is flanked by two pairs of lateral cusplets; the cusp
630 and cusplets are joined at their bases. The central cusp is somewhat compressed
631 labiolingually; the labial face is flattened and the lingual face is strongly convex. The occlusal
632 crest is labially displaced from the cusp centre and forms well developed cutting edges.
633 Moderately strong vertical ridges or cristae ascend the cusp from the cusp base both labially
634 and lingually; the ridges on the labial face of the cusp are stronger and less densely packed
635 than those on the lingual face, and they occasionally show bifurcation basally. The vertical
636 ridges on the mesial and distal parts of the lingual face of the central cusp have curved
637 trajectories as they ascend the cusp base. The lateral cusplet bases have similar cross-sectional
638 shapes to that of the central cusp, and similar vertical ridge distribution. The first or
639 intermediate lateral cusplet pair is smaller in size than the second or outermost pair. The tooth
640 base is incomplete, but the mesial and distal wings extend slightly beyond the bases of the

outermost lateral cusplet bases. In occlusal view, the base has two prominent, widely separated orolingual buttons with oval outlines elongated mesiodistally. Vascular foramina penetrate the root tissues around the bases of the orolingual buttons and in single rows around the labial border of the base, close to the lateral cusplet bases mesial and distal to the central cusp base, and between the orolingual buttons on the lingual shoulder of the base. In labial view, the base of the tooth is very shallow with two basally-projecting basolabial projections, each situated beneath one of the orolingual buttons. The labial margin of the base between these two projections is arched.

DGO25462 (Fig. 8B) is an isolated central cusp fragment which probably also belongs to *Glencartius costellatus*; the 0.8mm long fragment is compressed labiolingually, has well-defined cutting edges, and coarse, basally bifurcating vertical ridges on the somewhat flattened labial face.

Remarks and Occurrence: DGO 25459 is most likely a specimen of *Glencartius costellatus* (Traquair), a ctenacanthiform shark of undetermined familial status previously described from the Viséan of Glencartholm, Scotland (Traquair 1884; Moy-Thomas 1936; Ginter et al. 2010; Ginter and Skompski 2019), the Upper Viséan of Ticknall (Derbyshire, UK) and Todowa Grząba (Holy Cross Mountains, Poland) (Ginter et al. 2015), and Upper Viséan (V3a–c) limestones sampled in the Włodawa IG-4 borehole section of the Lublin-Lviv Basin (eastern Poland; Ginter and Skompski 2019). The Spanish specimen matches well in all respects with the material described and figured by Ginter et al. (2015, p. 915, figs. 9D, E) and Ginter and Skompski (2019, text-figs. 4C-E), although the Viséan material has more lateral cusplet pairs.

Superorder Cladodontomorphi Ginter, Hampe, et Duffin, 2010

Order Symmoriiformes Zangerl, 1981

Family Falcatidae Zangerl, 1990

Genus ***Denaea*** Pruvost, 1922

Type species: *Denaea fournieri* Pruvost, 1922.

Denaea sp.

Fig. 8(C)

Material: one isolated tooth, DGO 25458.

Description: DGO 25458 measures 0.9 mm mesiodistally and 0.5 mm labiolingually. The base outline is roughly pentagonal in occlusal and basal views, and the symmetrical crown comprises a central cusp flanked by two pairs of lateral cusplets, each of which is slightly curved lingually in lateral view. In this instance, the central cusp and lateral cusplets have rounded rather than labio-lingually compressed cross sections; their bases are well separated from each other and the cusp axes are mildly divergent apically. The coronal ornament is much reduced compared to that in DGO25459, comprising only a few indistinct, non-bifurcating vertical ridges ascending the lateral cusplets labially. There is no occlusal crest or cutting edge development. The base is shallow. A weak basolabial projection with a square outline is situated directly beneath the base of the central cusp. The base is relatively deeper than is the case in DGO25459. The lateral wings are relatively bulbous and deep with rounded lateral margins. A single, very low, weakly developed orolingual button is situated at the labial midpoint of the base and is perforated by a foramen for the main vascular canal on the basolabial margin, and again in the centre of the occlusal surface of the base.

Remarks: The combination of characters in this specimen, especially the shallow base, weak articulation device and delicate cusps with circular cross-section, suggests that it should be allocated to the falcatid symmoriiform shark, *Denaea* sp. The lack of clearly defined coronal ornament prevents assignation of the Spanish specimen to any particular species of the genus.

Occurrence: *Denaea* was originally erected for articulated specimens from the Viséan of Denée, Belgium (Pruvost, 1922), but a number of tooth based species have subsequently been

691 established, giving the genus a range from the Fammenian (Late Devonian) to the Bashkirian
692 (Ginter et al. 2010, p. 66).
693
694 Subclass Subterbranchialia Zangerl, 1979
695 Superorder Holocephali Bonaparte, 1832-1841
696 Order Helodontiformes Patterson, 1965
697 Family Helodontidae Patterson, 1965
698 Genus ***Helodus*** Agassiz, 1838
699 **Type species:** *Helodus simplex* Agassiz, 1838.
700 *Helodus* sp.
701 Fig. 8(D)
702 **Material:** a single isolated tooth fragment, DGO 25454.
703 **Description:** Heavily worn, the fragment measures approximately 0.8mm across its largest
704 dimension and consists of a broken, rather low and tumid cusp from the central part of the
705 crown. The hypermineralised tissue of the crown is clearly visible, but further taxonomically
706 useful morphological details are lacking.
707 **Remarks and Occurrence:** *Helodus* is the sole member of the holocephalan Order
708 Helodontiformes. Ranging from Late Devonian to Early Permian and represented by a large
709 number of species, *Helodus* is a fairly common component of marine Carboniferous
710 successions (Stahl 1999).
711
712 Elasmobranchii indet. Scales
713 Figs. 8(E–Q)
714 **Material:** numerous isolated scales belonging to several morphotypes, including DGO
715 25441-25442, 25456-25457, 25463-25464, 25466-25467, 25469-25470, 25477-25478, 25480.

716 Morphotype 1: placoid scales

717 Figs. 8(E-O, Q)

718 **Description:** Placoid scales (also known as dermal denticles) are non-growing scales which
719 have a simple crown connected to a basal plate by means of a stalk-like neck. The dermal
720 denticles from the San Emiliano Formation all have posteriorly-directed crowns with a single
721 cusp. The tip of the cusp may be rounded (e.g. DGO 25451, DGO 25456; Figs. 8F, G) or
722 pointed. In the pointed examples, the cusp may be acutely pointed (DGO 25457, DGO 25467;
723 Figs. 8H, K), very acutely pointed (DGO 25480; Fig. 8O), or relatively obtusely pointed
724 (DGO 25468, DGO 25478; Fig. 8N). The crown is usually ornamented by a series of vertical
725 striations which usually arise from the basal plate, ascend the neck and then encroach onto the
726 anterior face of the crown base. The lateral margins of the cusp are often accentuated with
727 lateral ridges (e.g. DGO 25451, DGO 25469, DGO 25470, DGO 25477; Figs. F, I, L, M).

728 The vertical ridges may be very weak and impersistent (e.g. DGO 25456, DGO 25463:
729 Figs. 8E, G) or, more commonly, much stronger. In some cases, especially those with acutely
730 pointed cusps, there is a single well-developed, rounded ridge located centrally on the anterior
731 border of the cusp (e.g. DGO 25467, DGO 25469, DGO 25470, DGO 25477; Figs 8K, I, L,
732 M), and occasionally surmounted by a single or even a double sharp crest (DGO 25469 and
733 DGO 25480 respectively; Figs. 8L, O). Occasionally, very strong ridges are also developed
734 posteriorly (DGO 25466; Fig. 8J). In at least one example, the ridge pattern is quite complex
735 with at least four clearly discernible ridges, each bearing one or even two crests (DGO 25457;
736 Fig. 8H). In one instance (DGO 25464; Fig. 8Q) the rather flat crown is surrounded by coarse
737 ridges.

738 The neck may be quite deeply incised and relatively fragile (e.g. DGO 25451, DGO
739 25463; Figs. 8E, F) or quite thick and robust (e.g. DGO 25457, DGO 25466; Figs. 8H, J).

740 The basal plate is sometimes quite compact with conservative margins (e.g. DGO 25466,
741 DGO 25480; Figs 8H, O), while in other instances, it is considerably flared and bears
742 numerous long, thin denticulations, especially posteriorly (e.g. DGO 25469, DGO 25470;
743 Figs 8L, M).
744
745 Morphotype 2: ctenacanthiform scales
746 Fig. 8(P)
747 **Description:** DGO 25452 is an example of a large (0.8 mm wide) ctenacanthiform scale. The
748 crown of the scale comprises at least two rough longitudinal rows of fused cusps, which
749 reflect the growing nature of the scale. The most recently added cusps are situated on the
750 anterior face. Each of these cusps is unicuspid with a lanceolate, sharply pointed outline. The
751 anterior face of each cusp is marked by strong vertical ridges, which ascend the cusp from the
752 base of the neck, terminate just below the cusp apex, and converge and fuse apically. The
753 lateral margins of each cusp are defined by strong vertical ridges. The neck of the scale is
754 only slightly incised, and the base is very compact, not extending significantly beyond the
755 bounds of the coronal area.
756 These scales compare well with those figured by Ginter and Skompski (2019, text-fig.
757 6F) for *Glencartius costellatus* from the Upper Viséan limestones in the Włodawa IG-4
758 borehole, Lublin-Lviv Basin.
759
760 Class Acanthodii Owen, 1846
761 Order Acanthodiformes Berg, 1940
762 *Incertae familiae*
763 Fig. 8(AE)
764 **Material:** one isolated scale, DGO 25476.

765 **Description:** DGO 25476 is an isolated scale of *Acanthodes* type, measuring approximately
766 0.5mm across the widest diameter. Roughly diamond-shaped in surface view, the
767 unornamented outer surface is separated from the robust base by a prominent groove. The
768 outline of the base matches that of the crown, but is slightly larger. The base displays a
769 number of concentric growth lines on the lateral walls and is unevenly thickened with a
770 convex underside.
771
772 Class Osteichthyes Huxley, 1880
773 Subclass Actinopterygii Woodward, 1891
774 Order Palaeonisciformes Jarvik, 1961
775 Suborder Palaeoniscoidea Nelson, 2006
776 Undetermined palaeoniscoids
777 Figs. 8(R–Z, AA–AD, AF–AG)
778 **Material:** Osteichthyans are represented in the fauna by tooth-bearing bones, isolated teeth
779 and isolated scales.
780 **Description:** So far as can be determined, the isolated teeth and tooth-bearing bones all
781 belong to the same, as yet unidentified taxon. The bone fragments vary in size and shape from
782 0.7 mm to 1.5 mm in length, and from roughly triangular (DGO 25479, DGO 25484; Figs 8R,
783 S) to an elongate rectangle (DGO 25454, DGO 25460, DGO 25461; Figs 8AB, Z). The
784 identity of the bone fragments has not been determined. The number of teeth and tooth bases
785 represented on the fragments varies from 6 (DGO 25479, DGO 25480; Fig. 8S) to 24 (DGO
786 25461; Fig. 8Z). The teeth are arranged in roughly linear series on the biting surfaces of the
787 bones and each tooth has a circular to slightly oval cross-section. The shafts of the teeth may
788 be smooth (e.g. DGO 25460; Fig. 8AB) or ornamented by a series of very fine vertical
789 striations (e.g. DGO 25453; Fig. 8AA), and are generally parallel-sided. The occlusal surface

790 is marked by an acrodin pad, which may present a simple central apical cusp, a slightly
791 divided apical cusp (DGO 25460; Fig. 8AB), a straight transverse ridge (DGO 25461; Fig.
792 8Z), a somewhat curved transverse ridge (DGO 25461) or a complex star-shaped cusp (DGO
793 25479; Fig. 8S).

794 These morphologies are matched in general terms by those of the isolated teeth, which
795 may have circular (DGO 25483; Fig. 8X) or more oval cross-sections (DGO 25485; Fig. 8W)
796 and parallel-sided (DGO 25485; Fig. 8W) or tapering shafts (DGO 25465, DGO 25483; Figs.
797 8X, Y).

798 The scales in the collection vary from regular rhomboidal (DGO 25472; Fig. 8U) to
799 more elongate shapes (DGO 25471, DGO 25482; Figs. 8T, V). In complete specimens the
800 outer surface of the scale is relatively smooth with a series of short microscopic ridges
801 covering the scale surface and oriented parallel to the diagonal from the upper posterior
802 corner of the scale to the lower anterior corner. Some of these scales are perforated with
803 channels of the lateral line sensory canal (DGO 25471, DGO 25472; Figs. 8U, V). A series of
804 oblique folds may be present along the presumed dorsal border of the scale (DGO 25471,
805 DGO 25472; Figs. 8U, V), and a series of several prominent ridges may be developed parallel
806 to the presumed posterior border (DGO 25471; Fig. 8V). Some fragmentary specimens
807 consist of a series of parallel ridges, which probably represent the partial remains of the
808 posterior borders of former larger scales (DGO 25474, DGO 25475; Figs. 8AC, AD).
809

810 **6. Palaeoecological, taphonomical and palaeobiogeographical remarks**

811 The late Bashkirian faunal assemblage from Mina Profunda consists of skeletal parts
812 of benthic organisms (e.g., brachiopods, echinoderms, bryozoans) along with nektonic
813 elements (conodonts, sharks). The brachiopod assemblage fits into the shallow-water faunas
814 of Martínez Chacón and Winkler Prins (1993), characterized by rich associations that lived in

well-oxygenated warm waters. The Linguloidea genera and the small Chonetidina, typical of the quiet-water faunas of the same authors, occur in the shallow-water faunas as well (Martínez Chacón and Winkler Prins, 1993).

Different life habits have been proposed for the micro-rhynchonellid *Lambdarina*, characterized by a relatively big pedicle foramen with respect to the small-sized shell, leading to the possession of a functional pedicle throughout its lifetime. Brunton and Champion (1974) suggested an epiplanktonic habit with the pedicle attached to plants or animals. It has also been proposed that *Lambdarina* lived in clusters, either in relatively low-energy carbonate environments (Nazer,1983) or occupying small crevices on a rocky bottom (Morris, 1994). Basset and Bryant (1993) agree with Grant (1988) in that the foramen size is no guide to pedicle form and function, seeing no reason to favour an attachment to hard substrates or an epiplanktonic mode of life and suggesting that a rhizoid pedicle would permit *L. glaphyra* Basset et Bryant to colonize low-energy soft bottoms.

The presence of one circular, minute predatory boring per specimen, probably produced by small gastropods, is characteristic of lambdarinids and cardiarinids (Cooper, 1956; Brunton and Champion, 1974; Grant, 1988; Basset and Bryant, 1993; Morris, 1994; Martínez Chacón, 1997). Remarkably, no clear predatory borings have been observed in the specimens of *L. winklerprinsi* nov. sp., as in *L. granti* Nazer and *L. jugowiensis* Muszer.

Noticeably, apart from broken and disarticulated shells, brachiopods from the Mina Profunda appear as intact specimens, with the shells not filled with sediment. This mode of occurrence suggests that their transport and their burial possibly occurred soon after, or was directly related to their death (cf. Underwood, 1994; Brett, 2003). The facies features of the hosting beds suggest that they were deposited by traction-plus-fallout or fallout sedimentation from relatively dilute gravity flows transporting grains and mud (see Middleton and Hampton, 1973; Lowe, 1982; amongst others). Field relationships suggest that these sediment gravity

840 flows would have been mostly sourced from a nearby shallow-water area and that they
841 transported their load into a low-energy, partially restricted slope-to-basin environment. Thus,
842 it is likely that the gravity flows entrained the living brachiopods from the sea floor and
843 transported them into the deep-water setting where they were deposited as part of the turbidite
844 beds.

845 Another example of gravity-flow deposits from a deep-water setting containing
846 transported shallow-water fauna, including Lambdarinids and associated microbrachiopods, is
847 represented by the middle Tournaisian Muhua Formation of South China (Baliński, 1999;
848 Ginter and Sun, 2007; Baliński and Sun, 2008).

849 The palaeobiogeographic connections of the late Bashkirian–early Moscovian
850 Cantabrian brachiopods (Valdeteja, San Emiliano and Calizas del Cuera formations) have
851 been discussed in Martínez Chacón and Winkler Prins (1993, 2009, 2015). The main
852 relationships are with Central Europe, Donbass (Ukraine) and the Moscow Syneclise
853 (Russia), in agreement with its palaeogeographical position in the western margin of the
854 Palaeotethys. There are also links with America, apparently established through the Urals and
855 the Arctic. However, as Martínez Chacón and Winkler Prins, (2015) have suggested, a
856 connection between the western Palaeotethys and the Panthalassa Ocean through the Iberian-
857 Midcontinent Seaway cannot be excluded, since Vai (2003) and García-Bellido and
858 Rodríguez (2005) pointed out that this seaway did not close until Kasimovian times.

859 The fish and conodont assemblage from Mina Profunda were likely either pelagic or
860 benthopelagic, being widely represented in different regions of the world. Chondrichthyan
861 cladodonts probably hunted close to the sea surface, and thus their remains could occur in
862 very different environments, from shallow- to deep-sea biofacies. The presence of *Helodus* is
863 consistent with a shallow-water environment (Roelofs et al. 2016), following the

chondrichthyan biofacies model of Ginter (2000, 2001). Conversely, the cladodont teeth of *Denaea* is associated with basinal carbonate facies in northern Europe (Ginter et al. 2015).

7. Conclusions

The application of micropalaeontological techniques to the upper Bashkirian Caliza Masiva of the San Emiliano Formation (Cantabrian Zone) recalls how the difficulties to extract the fossils without the appropriate techniques and certain preservation conditions produce biases in the fossil record, distorting the patterns of diversity over time. The studied faunal assemblage is primarily characterized by phosphatic (*Langella, Orbiculoidea*) and silicified calcareous articulate microbrachiopods (chonetid, *Lambdarina, Composita, Crurithyris*, terebratulids), frequently under-represented due to their low fossilization potential. The exceptional record of the microbrachiopod *Lambdarina winklerprinsi* nov. sp. in our samples contributes to filling the very discontinuous Viséan–late Permian fossil records of this genus. The abundant and diverse fish remains obtained from the same insoluble residues are consistent with a highly efficient marine ecosystem during the sedimentation of the Caliza Masiva. The accompanying conodont elements are scarce, though indicative of a late Bashkirian age (*Idiognathoides sulcatus parvus* Zone) for the faunal assemblage.

Acknowledgements

Dr Gabriela Cisterna (CONICET-UNLAR), Dr Michał Ginter (University of Warsaw), Dr Tamara Nemyrovska (National Academy of Sciences of Ukraine), an anonymous reviewer, and the Associate-Editor Dr Bertrand Lefebvre, critically appraised the manuscript. Thanks are also given to Prof. Luis C. Sánchez de Posada (University of Oviedo) for the critical reading of the manuscript. GGV greatly thanks CONICET and the Geology Department of the Oviedo University for a visiting research fellowship. Sampling was done during a study

for SIEMCALSA (Project FUO-315-17) carried out by JLA, LPF and GGV. Financial support by Project GRUPIN IDI/3018/000216 is also acknowledged.

References

Agassiz, J.L.R., 1837–1843. Recherches sur les poissons fossiles 3. Neuchâtel et Soleure, Petitpierre.

Alonso, J.L., Marcos, A., Suárez, A., 2009. Paleogeographic inversion resulting from large out of sequence breaching thrusts: The León Fault (Cantabrian Zone, NW Iberia). A new picture of the external Variscan Thrust Belt in the Ibero-Armorican Arc. Geologica Acta 7, 451–473.

Alonso, J.L., Marcos, A., Villa, E., Suárez, A., Merino-Tomé, O.A., Fernández, L.P., 2015. Mélanges and other types of block-in-matrix formations in the Cantabrian Zone (Variscan Orogen, northwest Spain): origin and significance. International Geology Review 57, 563–580.

Alonso, J.L., Suárez, A., Rodríguez Fernández, L.R., Farías, P., Villegas, F.J., 1989. Mapa Geológico de España E. 1:50.000, Hoja Nº 103 (Pola de Gordón). Instituto Geológico y Minero de España.

Baliński, A., 1999. Brachiopods and conodonts from the Early Carboniferous of South China. Acta Palaeontologica Polonica 44, 437–451.

Baliński, A., Sun, Y., 2008. Micromorphic brachiopods from the Lower Carboniferous of South China and their life habits. In: Harper, D.A., Long S., Nielsen, C. (eds.), Fossil and recent Brachiopoda. Fossils and Strata 54, pp. 105–115.

Bassett, M.G., Bryant, C., 1993. The micromorphic rhynchonelloidean brachiopod *Lambdarina* from the type Dinantian. Journal of Paleontology 67, 518–527.

Bowman, M.B.J., 1982. The stratigraphy of the San Emiliano Formation and its relationships to other Namurian/Westphalian A sequences in the Cantabrian Mts., NW Spain. Trabajos de Geología 12, 23–35.

Brett, C.E., 2003. Taphonomy: Sedimentological Implications of Fossil Preservation, in: Middleton, G.V., Church, M.J., Coniglio, M., Hardie, L.A., Longstaffe F.J. (Eds.), Encyclopedia of Sediments and Sedimentary Rocks. Springer, Dordrecht, pp. 723–729.

Brouwer, A., van Ginkel, A.C., 1964. La succession carbonifère dans la partie meridionales des Montagnes Cantabriques (Espagne du Nord-Ouest). V Congrès International Stratigraphie et Géologie du Carbonifère, Paris 1963. Compte Rendu 1, pp. 307–319.

Brunton, C.H.C., 1984. Silicifed brachiopods from the Viséan of County Fermanagh, Ireland (III). Rhynchonellids, Spiriferids and Terebratulids. Bulletin of the British Museum (Natural History), Geology 38, 27–130.

Brunton, C.H.C., Champion, C., 1974. A Lower Carboniferous brachiopod fauna from the Manifold Valley, Staffordshire. Palaeontology 17, 811–840.

Butt, S.H., Briggs, D.E.G., 2011. Chapter 11: Silicification Through Time, in: Allison, P.A. and Bottjer, D.J. (Eds.), Taphonomy: Process and Bias Through Time. Topics in Geobiology 32. Springer Science+Business Media B.V., Berlin, pp. 411–434

Carballeira, J., Corrales, I., Valladares, l., Naval, A., Ruiz, F., Lorenzo, S., Martínez Chacón, M.L., Méndez, C., Sánchez de Posada, L.C., Truyols, J., 1985. Aportaciones al conocimiento de la estratigrafía de la Formación San Emiliano (Carbonífero, Cordillera Cantábrica) en su área-tipo. X Congres lnternational de Stratigraphie et de Géologie du Carbonifere, Madrid 1983. Compte Rendu 1, pp. 345–362.

Cooper, G.A., 1956. New Pennsylvanian brachiopods. Journal of Paleontology 30, 521–530.

Davidson, T., 1848. Mémoire sur les Brachiopodes du Système Silurien supérieur de l'Angleterre. Société Géologique de France, Bulletin (séries 2) 5, 309–338, 370–374.

de Oliveira, E., 1930. Fosseis Marinhos na Série Itararé no Estado de Santa Catarina. Anais da Academia Brasileira de Ciências 2, 18–21.

Fernández, L.P., 1990. Estratigrafía, sedimentología y paleogeografía de la región de Riosa, Quirós y Teverga-San Emiliano. Ph.D. thesis, Universidad de Oviedo, 322 pp. (unpubl.).

Fernández, L.P., 1993. La Formación San Emiliano (Carbonífero de la Zona Cantábrica, NO de España): Estratigrafía y extensión lateral. Algunas implicaciones paleogeográficas. Trabajos de Geología 19, 97–122.

Fleming, J., 1828. A history of British animals, exhibiting their descriptive characters and systematic arrangement of the genera and species of Quadrupeds, Birds, Reptiles, Fishes, Mollusca, and Radiata of the United Kingdom Bell & Bradfute, Edinburgh.

García Bellido, D.C., Rodríguez, S., 2005. Palaeobiogeographical relationships of poriferan and coral assemblages during the late Carboniferous and the closure of the western Palaeotethys Sea Panthalassan Ocean connection. Palaeogeography, Palaeoclimatology, Palaeoecology 219, 321–331.

954 Ginter, M., 2000. Late Famennian pelagic shark assemblages. Acta Geologica Polonica 50,
955 369–386.
956 Ginter, M., 2001. Chondrichthyan Biofacies in the Late Famennian of Utah and Nevada.
957 Journal of Vertebrate Paleontology 21, 714–729.
958 Ginter, M., Duffin, C.J., Dean, M.T., Korn, D., 2015. Late Viséan pelagic chondrichthyans
959 from northern Europe. Acta Palaeontologica Polonica 60, 899–922.
960 Ginter, M., Hampe, O., Duffin, C.J., 2010. Chondrichthyes. Paleozoic Elasmobranchii: Teeth,
961 in: Schultze, H.-P. (Ed.), Handbook of Paleoichthyology, Vol. 3D. Friedrich Pfeil,
962 München. 168 pp.
963 Ginter, M., Skompski, S., 2019. The squamation of "Ctenacanthus" costellatus
964 (Chondrichthyes: Ctenacanthiformes) from the Carboniferous of Lublin area, south-
965 eastern Poland. Acta Geologica Polonica 69, 571–582.
966 Ginter, M., Sun, Y., 2007. Chondrichthyan remains from the Lower Carboniferous of Muhua,
967 southern China. Acta Palaeontologica Polonica 52, 705–727.
968 Grant, R.E., 1988. The family Cardiarinidae (late Paleozoic rhynchonellid Brachiopoda).
969 Senckenbergiana Lethaea 69, 121–135.
970 Harris, R.W., Hollingsworth, R.V., 1933. New Pennsylvanian conodonts from Oklahoma.
971 American Journal of Science, Series 5, 25, 193–204.
972 Higgins, A.C., 1975. Conodont zonation of the late Viséan -early Westphalian strata of the
973 south and central Pennines of northern England. Bulletin of the Geological Survey of
974 Great Britain 53, 1–90.
975 Higgins, A.C., Bouckaert, J., 1968. Conodont stratigraphy and paleontology of the Namurian
976 of Belgium. Service Géologique de Belgique, Mémoire 10, 1–64.
977 Ivanov, A.P., 1935, Fauna brakhiopod srednego i verkhnego karbona Podrnoskovnogo
978 basseina. Chast 1. Productidae Gray, Vypusk 1. Productinae Shuch. em. Paeck.
979 [Brachiopods of the Middle and Upper Carboniferous of the Moscow Basin. Part 1.
980 Productidae Gray]. Moskovskyi Geologicheskii Trest, Trudy (Moscow) 8 (in Russian).
981 Lane, N.G., 1963. A silicified Morrowan brachiopod faunule from the Bird Spring Formation,
982 southern Nevada. Journal of Paleontology 37, 379–392.
983 Legrand-Blain, M., 1984. Étude paléontologique. In: Legrand-Blain, M., Delvolvé, J.J.,
984 Perret, M.F. Les brachiopodes Carbonifères des Pyrénées Centrales Françaises. 2. Étude
985 des Orthida et des Spiriferida: Biostratigraphie, Paléoécologie. Geobios 17, 297–325.

Lowe, D.R., 1982. Sediment gravity flows; II, Depositional models with special reference to the deposits of high-density turbidity currents. Journal of Sedimentary Research 52, 279–297.

Martínez Chacón, M.L., 1978. Nuevos braquiópodos de la Formación San Emiliano (Cordillera Cantábrica, NO de España). Breviora Geologica Asturica 22, 17–32.

Martínez Chacón, M.L., 1979. Braquiópodos carboníferos de la Cordillera Cantábrica (Orthida, Strophomenida y Rhynchonellida). Memorias del Instituto Geológico y Minero de España 96, 1–291.

Martínez Chacón, M.L., 1990. Braquiópodos carboníferos dela costa E de Asturias (España). I: Orthida, Strophomenida, Rhynchonellida y Athyridida. Revista Española de Paleontología 5, 91–110.

Martínez Chacón, M.L., 1991. Braquiópodos carboníferos de la costa E de Asturias (España). II: Spiriferida y Terebratulida. Revista Española de Paleontología 6, 59–88.

Martínez Chacón, M.L., 1997. Braquiópodos silicificados viseenses de Los Santos de Maimona (Badajoz, SO de España). Geobios 30 (Supp. 1), 357–372.

Martínez Chacón, M.L., Bahamonde, J.R., 2008. Brachiopods from a steep-slope facies of a Pennsylvanian carbonate platform (Sierra del Cuera, Asturias, North Spain). Fossils and Strata 54, 133–143.

Martínez Chacón, M.L., Sánchez de Posada, L.C., 2018. Espiriféridos (Brachiopoda) del Bashkiriense superior (Pensilvánico) de la formación Valdeteja, Asturias (N de España). Trabajos de Geología 36, 311–346.

Martínez Chacón, M.L., Winkler Prins, C.F., 1985. The brachiopod fauna of the San Emiliano Formation (Cantabrian Mountains, NW Spain) and its connection with other areas. IX Congrès sur le Carbonifère, Champaign-Urbana, 1979. Compte Rendus 5, pp. 233–244.

Martínez Chacón, M.L., Winkler Prins, C.F., 1993. Carboniferous brachiopods and the palaeogeographic position of the Iberian Peninsula. XII Congrès International Stratigraphie et Géologie du Carbonifère, Buenos Aires 1991. Compte Rendus 1, pp. 573–580.

Martínez Chacón, M.L., Winkler Prins, C.F., 2007. Medio siglo de estudio de los braquiópodos del yacimiento de Latores (SO Oviedo). I Congreso de Estudios Asturianos, Oviedo 2006. Tomo 6, pp. 309–326.

Martínez Chacón, M.L., Winkler Prins, C.F., 2008. Some new Bashkirian (Carboniferous) brachiopods from Latores (Asturias, N Spain). Proceedings of the Royal Society of Victoria 120, 194–205.

1020 Martínez Chacón, M.L., Winkler Prins, C.F., 2009. Brachiopods from the Valdeteja
1021 Formation (Pennsylvanian; Cantabrian Mountains, NW Spain). Neues Jahrbuch für
1022 Geologie und Paläontologie Abhandlungen 252, 91–111.
1023 Martínez Chacón, M.L., Winkler Prins, C.F., 2015. Late Bashkirian-early Moscovian
1024 (Pennsylvanian) Productidae (Brachiopoda) from the Cantabrian Mountains (NW
1025 Spain). Geobios 48, 459–477.
1026 Méndez Fernández, C.A. 1990. Conodontos del Carbonífero Superior de la Cordillera
1027 Cantábrica. Ph.D Thesis, Universidad de Oviedo, 213 pp. (unpubl.).
1028 Middleton, G.V., Hampton, M.A. 1973. Sediment gravity flows: mechanics of flow and
1029 deposition, in: Middleton, G.V., Bouma, A. H. (eds.), Turbidites and Deep Water
1030 Sedimentation. Society for Sedimentary Geology, Pacific Section, Short Course Notes,
1031 Anaheim, pp. 1–38.
1032 Moore, L.R., Neves, R., Wagner, R.H., Wagner Gentis, C.H.T. 1971. The stratigraphy of
1033 Namurian and Westphalian rocks in the Villamanín area of Northern Leon, N. W.
1034 Spain. Trabajos de Geología 3, 307–363.
1035 Morris, P.G., 1994. Some new Lower Carboniferous cardiarinid brachiopods from the
1036 Milldale Limestones (Viséan, Chadian) of North Staffordshire, England. Neues
1037 Jahrbuch für Geologie und Paläontologie, Monatshefte 5, 267–276.
1038 Moy-Thomas, J.A., 1936. The structure and affinities of the fossil elasmobranch fishes from
1039 the Lower Carboniferous rocks of Glencartholm, Eskdale. Proceedings of the
1040 Zoological Society of London 1936, pp. 761–788.
1041 Muszer, J., 2014. A new species of Lambdarina (Rhynchonellida, Brachiopoda) from the
1042 Viséan of central Sudetes (Poland) and its phylogenetic position. Acta Geologica
1043 Polonica 64, 1–12.
1044 Nazer, R., 1983. *Lambdarina* (Rhynchonellacea) from the Upper Viséan of Queensland.
1045 Journal and Proceedings, Royal Society of New South Wales 116, 119–121.
1046 Nemyrovska, T.I., 1999. Bashkirian conodonts of the Donets Basin, Ukraine. Scripta
1047 Geologica 119, 1–115.
1048 Nemyrovska, T.I., 2017. Late Mississippian–Middle Pennsylvanian conodont zonation of
1049 Ukraine. Stratigraphy 14, 299–318.
1050 Nemyrovska, T.I., Hu, K., 2018. Conodont association of the Bashkirian-Moscovian
1051 boundary interval of the Donets Basin, Ukraine. Spanish Journal of Palaeontology 33,
1052 105–128.

1053 Pruvost, P., 1922. Description de Denaea fournieri, sélacien nouveau du Marbre noir de
1054 Denée. Part 2 of Fournier, G. and Pruvost, P., Découverte d'un poisson nouveau dans le
1055 marbre noir de Denée. Bulletin de Academie Royal de Bruxelles Série 5(8), 213–218.
1056 Qi, Y.-P., Lambert, L.L., Nemyrovska, T.I., Wang, X.-D., Hu, K.-Y., Wang, Q.-L., 2016. Late
1057 Bashkirian and early Moscovian conodonts from the Naqing section, Luodian, Guizhou,
1058 South China. Palaeoworld 25, 170–187.
1059 Riding, R., 1979. Donezella bioherms in the Carboniferous of the southern Cantabrian
1060 Mountains, Spain. Bulletin Centre Recherche Exploration–Production Elf–Aquitaine 3,
1061 787–794.
1062 Roelofs, B., Barham, M., Mory, A.J., Trinajstic, K., 2016. Late Devonian and Early
1063 Carboniferous chondrichthyans from the Fairfield Group, Canning Basin, Western
1064 Australia. Palaeontologia Electronica 19.1.4A, 1–28.
1065 Sánchez de Posada, L.C., Martínez Chacón, M.L., Méndez, C.A., Menéndez-Alvarez, J.R.,
1066 Río, L.M., Rodríguez, S., Truyols, J., Villa, E., 1996. El Carbonífero marino del ámbito
1067 astur-leonés (Zona Cantábrica): Síntesis paleontológica. Revista Española de
1068 Paleontología Nº Extraordinario, 82–96.
1069 Schubert, J.K., Kidder, D.L., Erwin, D.H., 1997. Silica-replaced fossils through the
1070 Phanerozoic. Geology 25, 1031–1034.
1071 Shumard, B.F., 1855. Description of a geological section on the Mississippi River, from St.
1072 Louis to Commerce. Geological Survey of Missouri, Annual Reports 1-2, 137–208.
1073 Sowerby, J., 1812-1815. The Mineral Conchology of Great Britain 1. Benjamin Meredith,
1074 London.
1075 Sowerby, J., 1822. The Mineral Conchology of Great Britain 4. Benjamin Meredith, London.
1076 Stahl, B.J., 1999. Chondrichthyes III. Holocephali. in: Schultze, H.-P. (ed.), Handbook of
1077 Paleoichthyology, Vol. 4. Friedrich Pfeil, München, 162 pp.
1078 Stone, J., 1987. Review of investigative techniques used in the study of conodonts, in: Austin,
1079 R.L. (ed), Conodonts: Investigative Techniques and Applications. Ellis Horwood
1080 Limited, Chichester, pp. 17–34.
1081 Sun, Y., Baliński, A., 2008. Silicified Mississippian brachiopods from Muhua, southern
1082 China: Lingulids, craniids, strophomenids, productids, orthotetids, and orthids. Acta
1083 Palaeontologica Polonica 53, 485–524.
1084 Traquair, R.H., 1884. Description of a fossil shark (*Ctenacanthus costellatus*) from the Lower
1085 Carboniferous rocks of Eskdale, Dumfrieshire. Geological Magazine 3, 3–8.

Truyols Santonja, J., Sánchez de Posada, L., 1983. El Carbonífero inferior y medio de la Región de Pliegues y Mantos, in: Martínez Díaz, C. (ed), Carbonífero y Pérmico de España. Instituto Geológico y Minero de España, Madrid, pp. 39–59.

Underwood, C.J., 1994. Faunal transport within event horizons in the British Upper Silurian. Geological Magazine 131, 485–498.

Vai, G.B., 2003. Development of the palaeogeography of Pangaea from Late Carboniferous to Early Permian. Palaeogeography, Palaeoclimatology, Palaeoecology 196, 125–155.

van Ginkel, A.C., 1965. Carboniferous fusulinids from the Cantabrian Mountains (Spain). Leidse Geologische Mededelingen 34, 5–225.

van Ginkel, A.C., 2014. The Villamanín Member of the San Emiliano Formation (Carboniferous, N Spain): Its age and fusulunoidean foraminifers. Geological Journal, National Academy of Sciences of Ukraine 2(347), 39–58.

van Ginkel, A.C., Villa E., 1996. Palaeontological data of the San Emiliano Formation (Cantabrian Mountains, Spain) and their significance in the Carboniferous chronostratigraphy. Geobios 29, 149–170.

Villa, E., Horvath, V., Martínez Chacón, M.L., Sánchez de Posada, L.C., 1988. Datos paleontológicos y edad de la sección de Villamanín (Carbonífero, C. Cantábrica NW de España). II Congreso Geológico de España, Granada, Comunicaciones 1, pp. 337–341.

von Schlotheim, E.F., 1816, Beiträge zur Naturgeschichte der Versteinerungen in Geognostischer Hinsicht. Denkschriften der Königlich Akademie der Wissenschaften zu Munchen für des Jahre 1816 und 1817 6, 13–36.

Wang, Z.-H., Qi, Y.-P., 2003. Upper Carboniferous (Pennsylvanian) conodonts from South Guizhou of China. Rivista Italiana di Paleontologia 109, 379–397.

Winkler Prins, C.F., 1968. Carboniferous Productidina and Chonetidina of the Cantabrian Mountains (NW Spain): Systematics, stratigraphy and palaeoecology. Leidse geologische mededelingen 43, 41–126.

Table and Figures captions

Table 1. Measurements (in mm) of some specimens of *Lambdarina winklerprinsi* nov. sp.

Fig. 1. Schematic geological map of the Cantabrian Zone with location of the study area (adapted from Alonso et al., 2015).

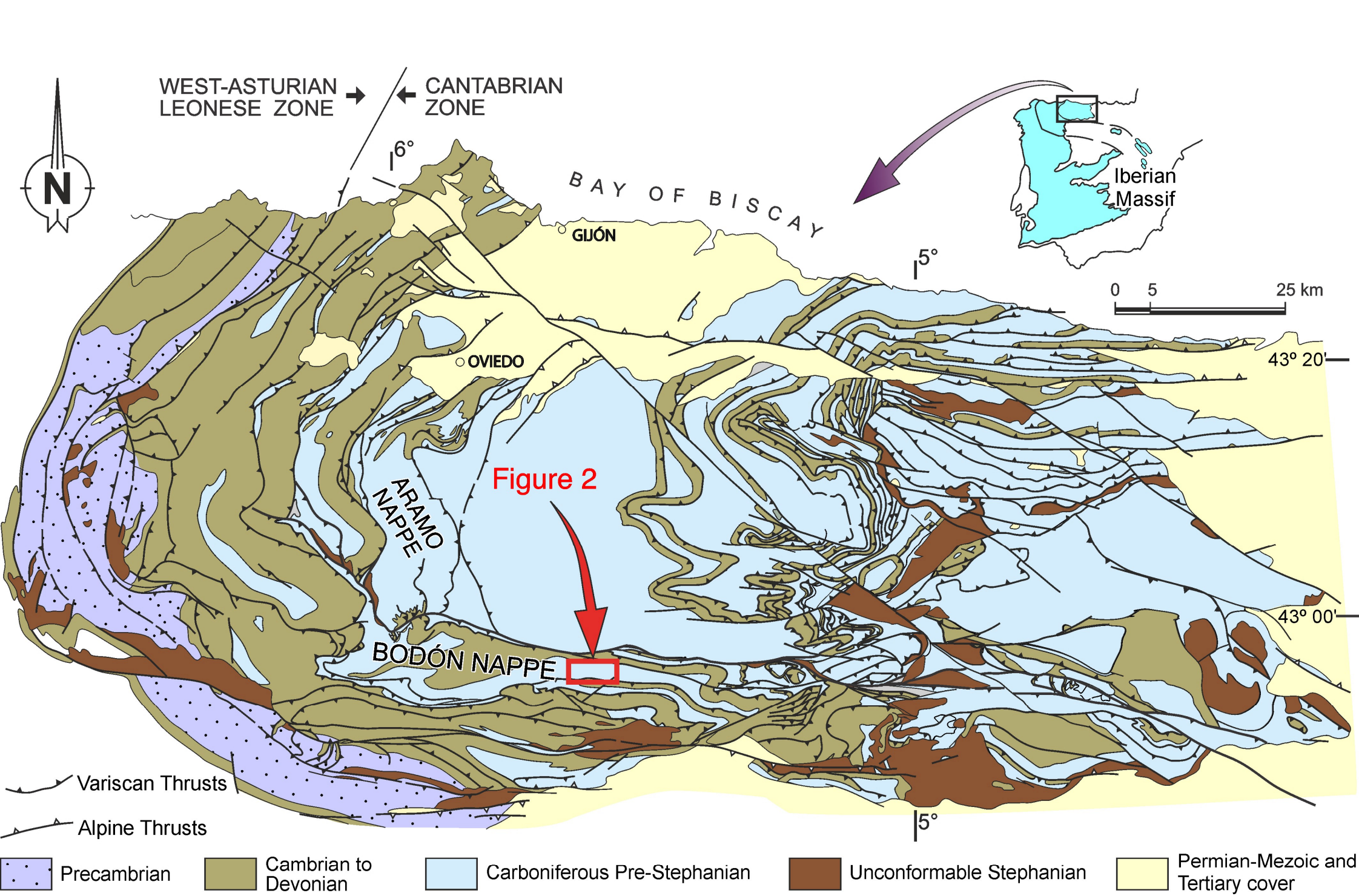
Fig. 2. Geological map of the Mina Profunda area (modified from Alonso et al. 1989) (**A**), and simplified stratigraphic column of the San Emiliano Formation in the study area (adapted from Fernández (1990) (**B**), with the location of the studied sample.

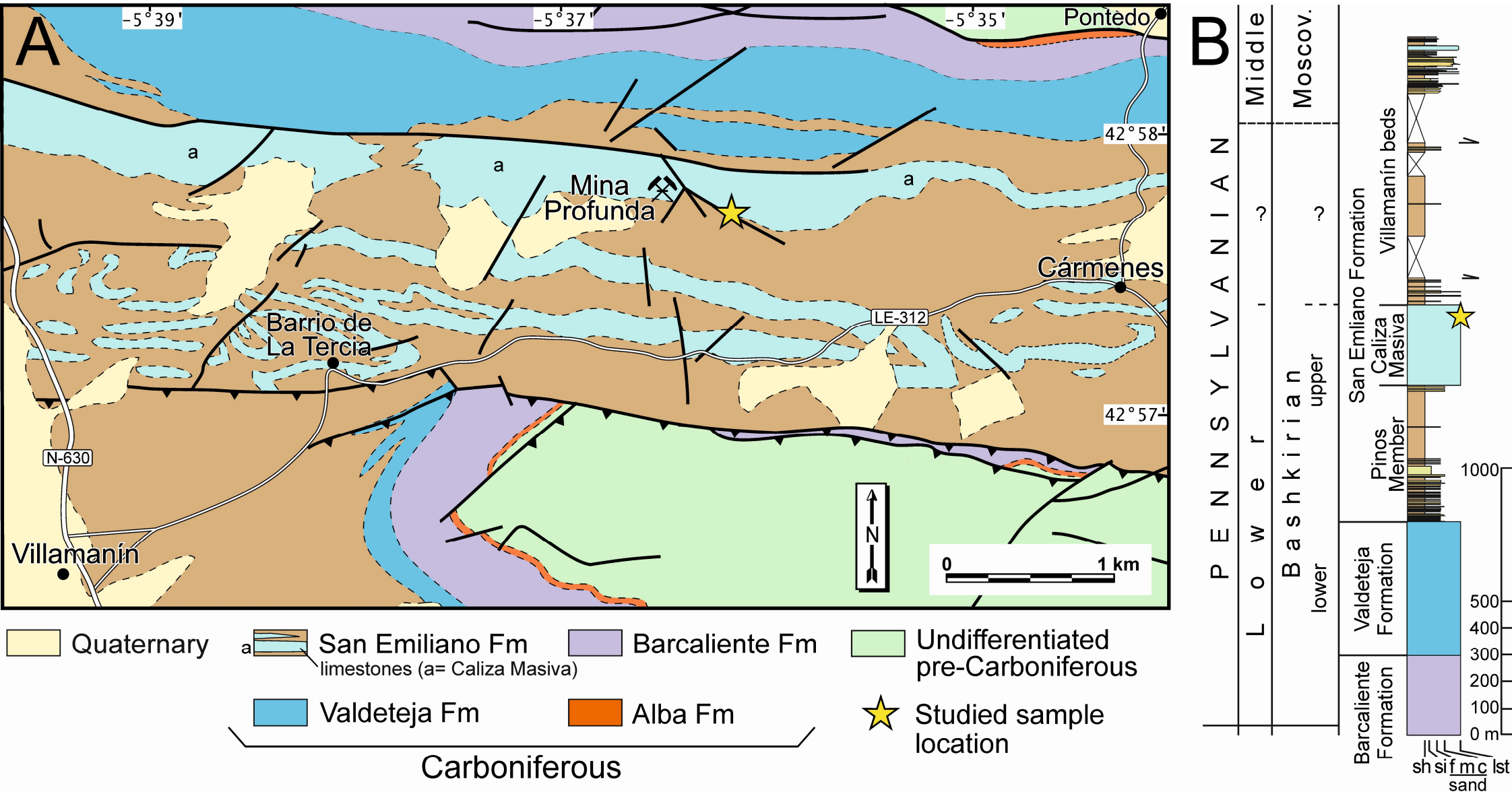
Fig. 3. Photomicrograph showing the texture of the sampled limestone. It consists of a skeletal and peloidal, intraclast-bearing packstone to grainstone. Notice the alternation of moderately to poorly sorted laminae containing sand- to gravel-size skeletal fragments and peloids (dark micritic rounded grains) with better sorted fine-sand-grade laminae mainly formed of sponge spicules and calcispheres (ct, chondrichthyan tooth; eq, equinoderm, mostly crinoids; sp, sponge spicules; br, brachiopods; f, forams; o, ostracods). Scale bar: 1 mm.

Fig. 4. A-C. *Langella*? sp. **A**. DGO 25486, ventral valve; **B-C**. DGO 25487-25488, dorsal valves. **D-F**. *Orbiculoidea* sp. **D**. DGO 25491, incomplete ventral valve; **E**. DGO 25490, incomplete ventral valve in external (E_1) and internal (E_2) views; **F**. DGO 25492, ventral valve of a juvenile specimen. **G**. Caenanopliinae gen. et sp. indet. DGO 25494, internal mould in ventral (G_1) and (G_2) dorsal views. **H-I, K-M**. *Crurithyris* cf. *urei* (Fleming, 1828). **H**. DGO 25519, internal mould of a ventral valve; **I**. DGO 25518, internal mould in dorsal view; **K**. DGO 25517, specimen in dorsal-posterior view, showing the high interarea; **L**. DGO 25520, posterior part of the interior of a dorsal valve showing the cardinal process and the posterior part of the crura; **M**. DGO 25524, dorsal internal mould. **J**. *Maemia* cf. *archboldi* Martínez Chacón et Winkler Prins, 2008, DGO 25496, ventral external view. **N.** *Composita*

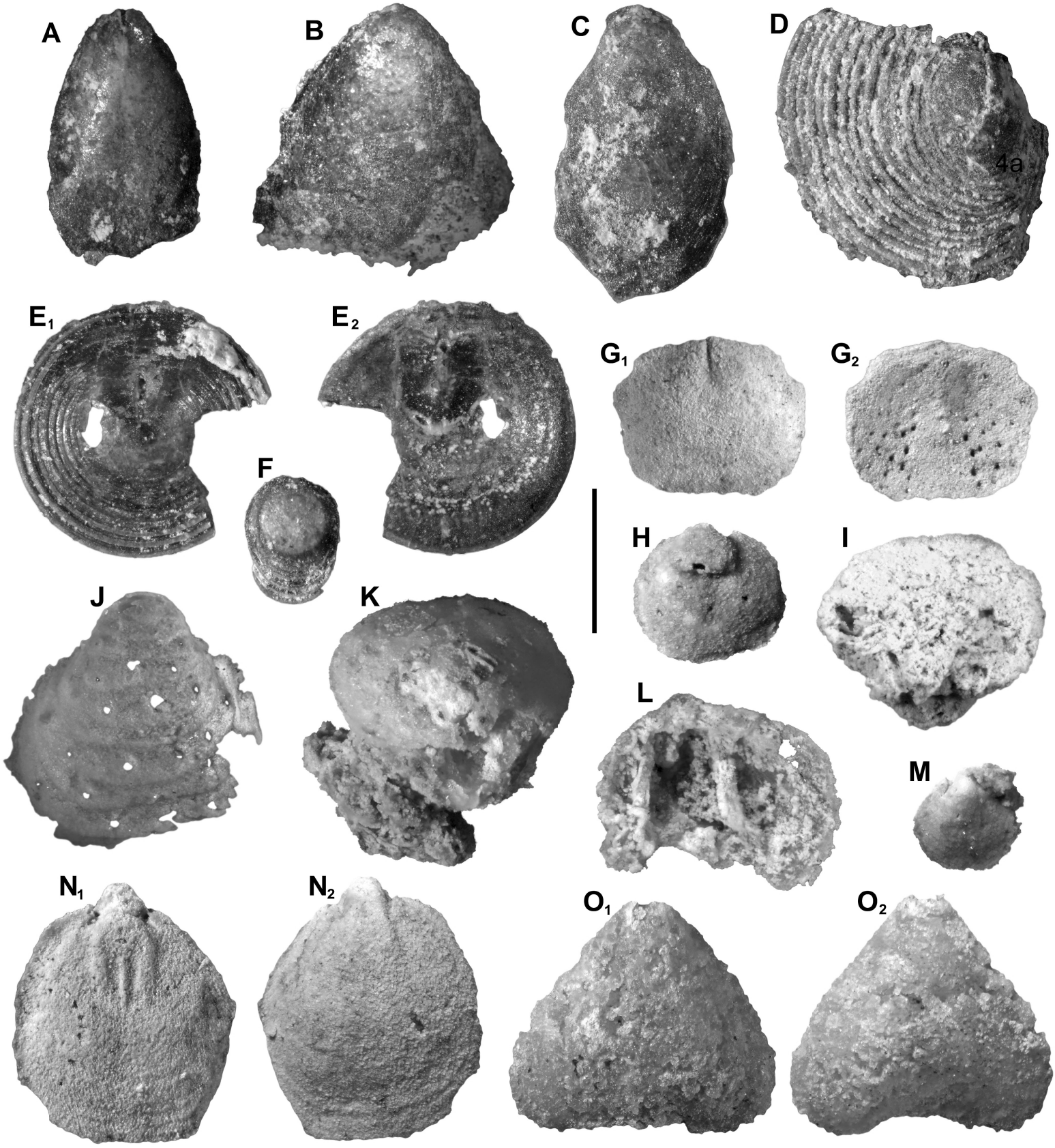
1143 sp., DGO 25515, internal mould in dorsal (N_1) and ventral (N_2) views. **O**. Terebratulidina gen.
1144 et sp. indet. 1, DGO 25531, specimen in ventral (O_1) and dorsal (O_2) views. Scale bar: 1 mm.
1145
1146 **Fig. 5. A**. Terebratulidina gen. et sp. indet. 2, DGO 25534, fragment of the anterior part of
1147 ventral valve. **B**. *Maemia* cf. *archboldi* Martínez Chacón et Winkler Prins, 2008, DGO 25495,
1148 specimen in ventral (B_1) and dorsal (B_2) views. **C**. *Spiriferellina* sp., DGO 25530, fragment of
1149 ventral valve. **D**. *Alexenia*? sp., DGO 25498, incomplete specimen in ventral view. **E**.
1150 *Anthracothyrina*? sp., DGO 25529, incomplete ventral internal mould. **F**. *Anthracospirifer*
1151 sp., DGO 25528, fragment of ventral valve. Scale bars: 2 mm.
1152
1153 **Fig. 6.** *Lambdarina winklerprinsi* nov. sp. **A**. DGO 25499, internal mould of a juvenile
1154 specimen in ventral (A_1) and dorsal (A_2) views. **B**. Holotype, specimen in ventral (B_1) and
1155 dorsal (B_2) views. **C**. DGO 25507, fragmentary internal mould in ventral (C_1) and dorsal (C_2)
1156 views. D. DGO 25503, ventral valve. **E**. DGO 25501, specimen in ventral (E_1) and dorsal (E_2)
1157 views. **F**. DGO 25502, incomplete specimen in ventral (F_1) and dorsal (F_2) views. **G**. DGO
1158 25500, specimen in ventral (G_1) and dorsal (G_2) views. **H**. DGO 25508, specimen with one of
1159 its lobes broken in ventral (H_1) and dorsal (H_2) views. **I**. DGO 25505, juvenile specimen in
1160 dorsal view. **J**. DGO 25504, juvenile specimen in dorsal view. Scale bar: 1 mm.
1161
1162 **Fig. 7.** *Idiognathoides sulcatus parvus* Higgins et Bouckaert, 1968, P_1 element, San Emiliano
1163 Formation, Mina Profunda, DGO 25535. Lateral (A) and oral (B) views. Scale bar: 0.01 mm.
1164
1165 **Fig. 8.** Ichthyoliths recovered from the Caliza Masiva member of the San Emiliano Formation
1166 (late Bashkirian), in the Mina Profunda area, NW Spain. **A.** *Glencartius costellatus* (Traquair,
1167 1884), DGO25459, oral view. **B.** Probably *Glencartius costellatus* (Traquair, 1884), DGO

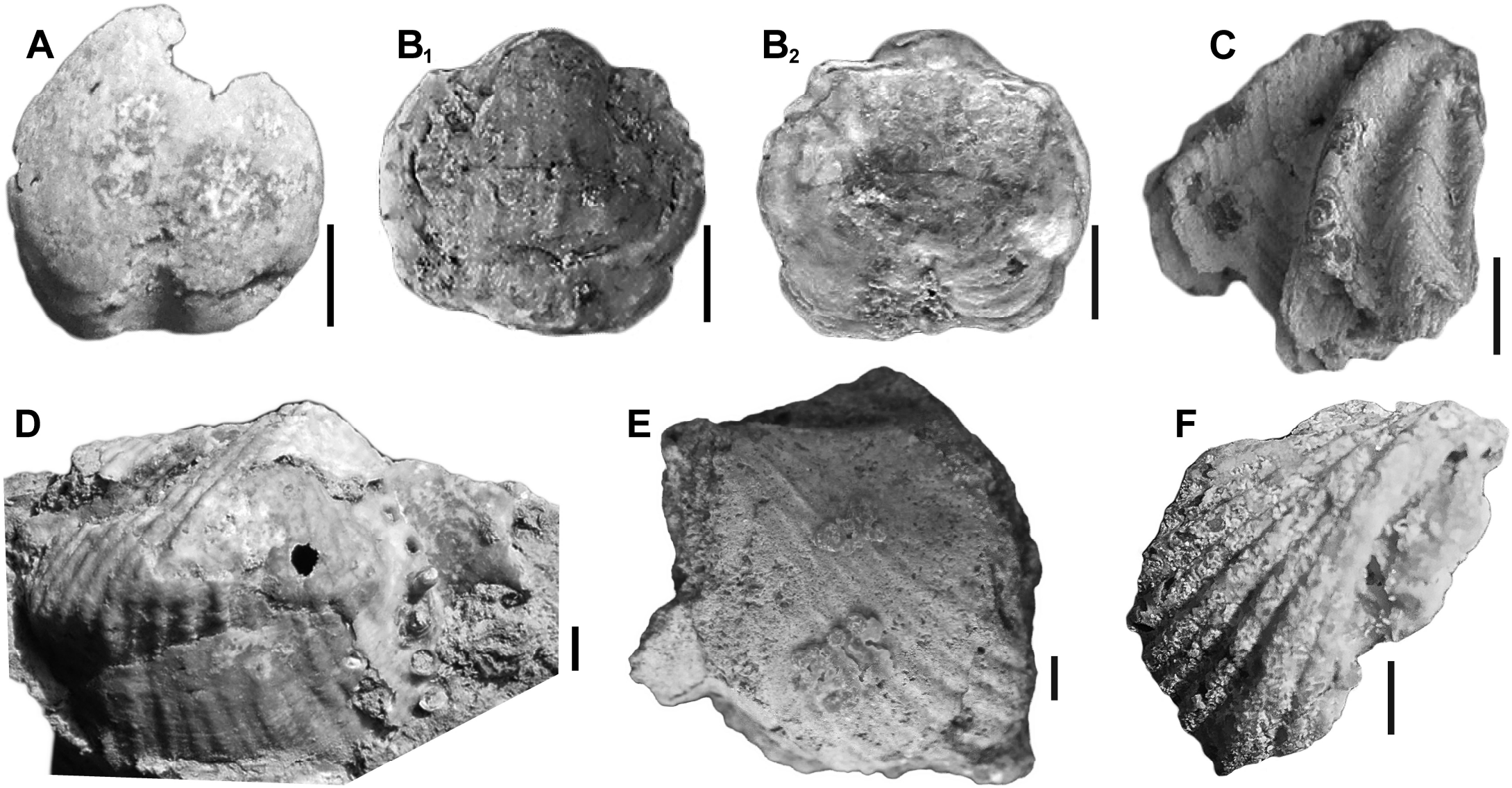
25462, labial view. **C.** *Denaea* sp., DGO25458, oral view. **D.** helodont tooth crown, DGO25454, oral view. **E.** placoid scale, DGO25463. **F.** placoid scale, DGO25451. **G.** placoid scale, DGO25456. **H.** placoid scale, DGO25457. **I**. placoid scale, DGO 25477. **J.** placoid scale, DGO 25466. **K.** placoid scale, DGO25467. **L.** placoid scale, DGO 25469. **M.** placoid scale, DGO 25470. **N.** placoid scale, DGO 25478. **O.** placoid scale, DGO25480. **P.** ctenacanthiform scale, DGO25452. **Q.** chondrichthyan scale, DGO25464. **R.** osteichthyan bone with teeth, DGO25484. **S.** osteichthyan bone with teeth, DGO25479. **T.** osteichthyan scale, DGO25482. **U.** osteichthyan scale, DGO25472. **V.** osteichthyan scale, DGO25471. **W.** isolated osteichthyan tooth, DGO25485. **X.** isolated osteichthyan tooth, DGO25483. **Y.** isolated osteichthyan tooth, DGO25465. **Z.** osteichthyan bone with teeth, DGO25461. **AA.** osteichthyan bone with teeth, DGO25453. **AB.** osteichthyan bone with teeth, DGO25460. **AC.** osteichthyan scale, DGO25474. **AD.** osteichthan scale, DGO25475. **AE.** acanthodian scale, DGO25476. **AF.** unidentified, DGO25473. **AG.** unidentified, DGO25468. Scale bars: 0.1 mm.

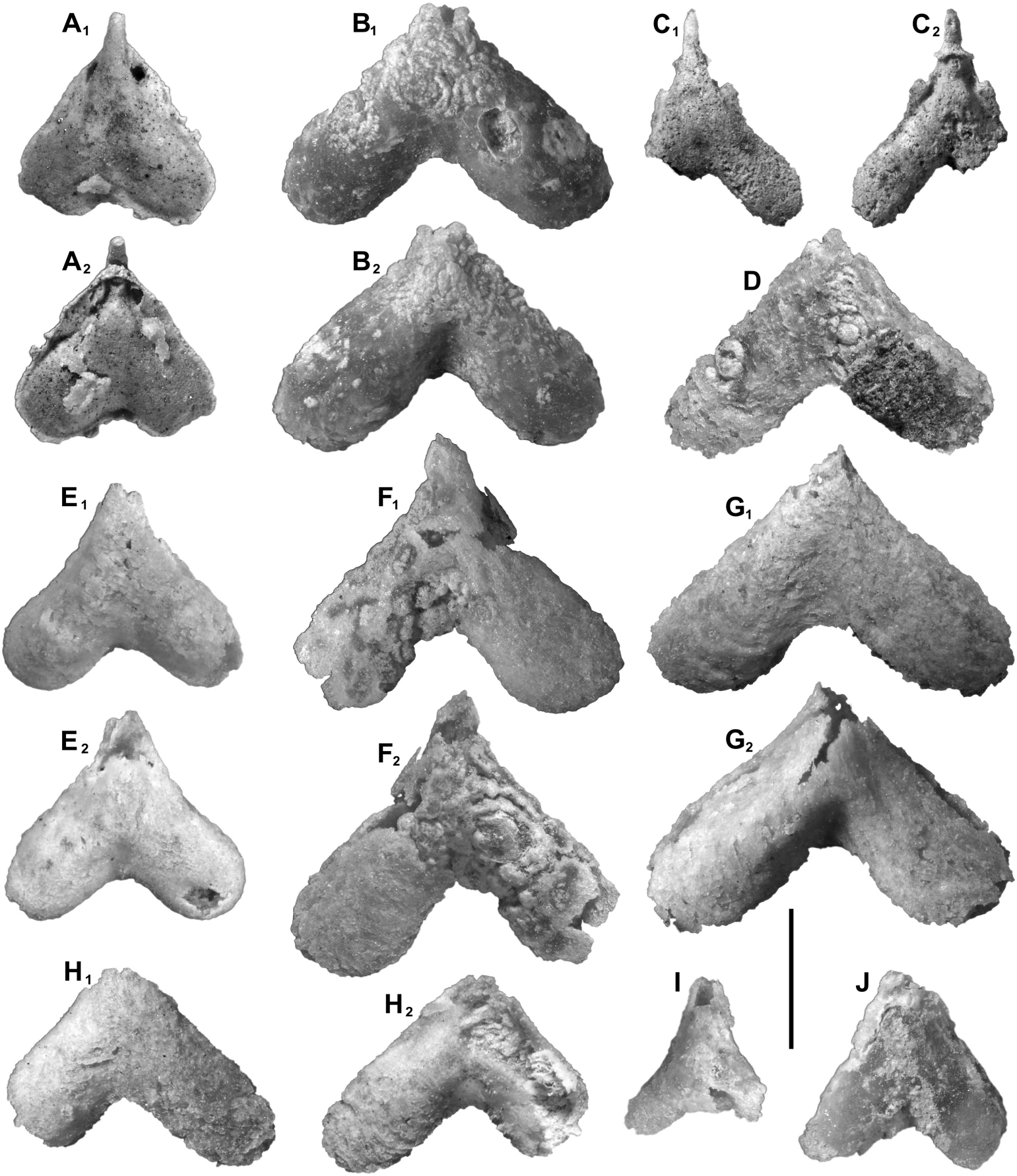

WEST-ASTURIAN LEONESE ZONE
CANTABRIAN ZONE
N
6°
5°
BAY OF BISCAY
GIJÓN
OVIEDO
Iberian Massif
0 5 25 km
43º 20'
43º 00'
ARAMO NAPPE
BODÓN NAPPE
Figure 2
Variscan Thrusts
Alpine Thrusts
Precambrian
Cambrian to Devonian
Carboniferous Pre-Stephanian
Unconformable Stephanian
Permian-Mezoic and Tertiary cover


A
-5°39'
-5°37'
-5°35'
Pontedo
42°58'
42°57'
a
Mina
Profunda
Cármenes
LE-312
Barrio de
La Tercia
N-630
Villamanín
N
0
1 km
Quaternary
San Emiliano Fm
limestones (a= Caliza Masiva)
Barcaliente Fm
Undifferentiated
pre-Carboniferous
Valdeteja Fm
Alba Fm
Studied sample
location
Carboniferous
B
PENNSYLVANIAN
Lower
Middle
Moscov.
Bashkirian
upper
lower
?
?
San Emliano Formation
Villamanín beds
Caliza
Masiva
Pinos
Member
Valdeteja
Formation
Barcaliente
Formation
1000
500
400
300
200
100
0 m
sh si f m c lst
sand

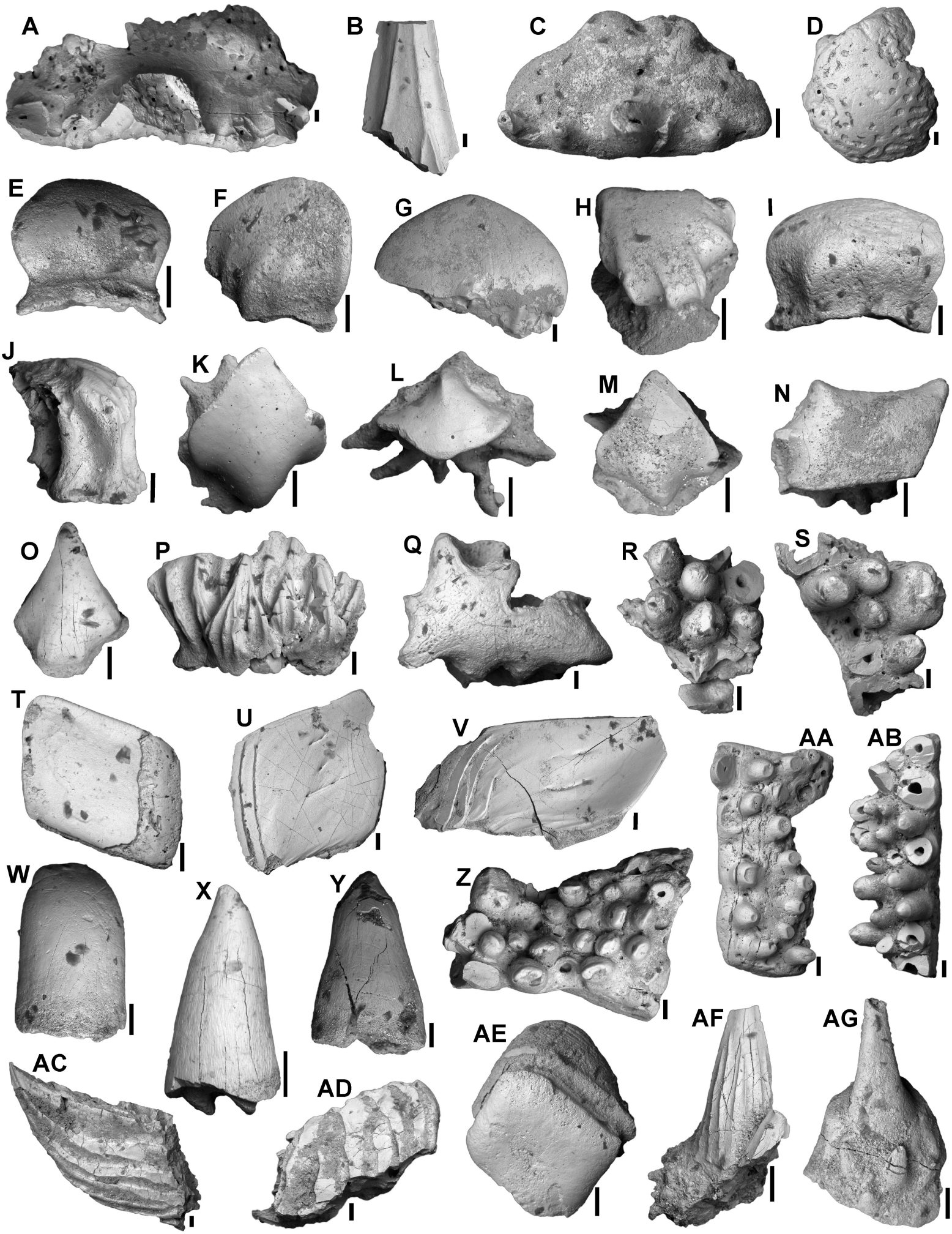

o
eq
eq
sp
f
ct
sp
br
f


A
B
C
D
4a
E1
E2
F
G1
G2
H
I
J
K
L
M
N1
N2
O1
O2


A
B1
B2
C
D
E
F


A1
B1
C1
C2
A2
B2
D
E1
F1
G1
E2
F2
G2
H1
H2
I
J


A
B


A
B
C
D
E
F
G
H
I
J
K
L
M
N
O
P
Q
R
S
T
U
V
AA
AB
W
X
Y
Z
AC
AD
AE
AF
AG